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THE UNIVERSITY OF ALBERTA

The Ichnology of the Lower Cambrian Gog Group, Lake Louise, Alberta

by

James P. A. Magwood B.Sc.

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF

Master of Science

Department of Geology

EDMONTON, ALBERTA
Fall, 1988

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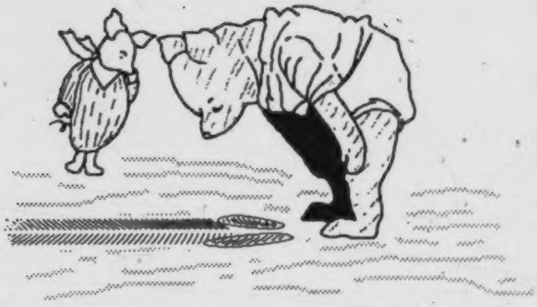

You can never tell with paw-marks!

Winnie the Pooh

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **The Ichnology of the Lower Cambrian Gog Group, Lake Louise Alberta**

submitted by **James P. A. Magwood**
in partial fulfilment of the requirements for the degree of
Master of Science

Supervisor

Date: October 10, 1988

ABSTRACT

The Gog Group is a thick, siliciclastic deposit composed of alternating units of cliff-forming, cross-bedded quartzites and recessive, thinly interbedded quartzites and shales. The resistant units comprise upper tidal flat deposits. They contain abundant shafts: *Arenicolites*, *Diplocraterion*, and *Skolithos* and sporadic simple burrows. The lower recessive unit comprises a shallow subtidal to intertidal deposit. The middle recessive unit grades up from lagoon and washover deposits into high energy, shallow subtidal deposits. The upper recessive unit consists of silt dominated, shallow subtidal and intertidal deposits with evidence for the development of stiff to firm substrates and reduced salinities. The subtidal and lower intertidal deposits contain diverse ichnofossil assemblages, including surface excavations: *Bergaueria*, *Cruziana*, *Didymaulichnus*, *Diplichnites*, *Dolopichnus*, *Monomorphichnus*, *Protichnites*, and *Rusophycus*; simple horizontal burrows: *Cochlichnus*, *Gordia*, *Palaeophycus*, *Planolites*, and *Trichophycus*; complex infaunal deposit-feeding structures: *Chondrites*, *Phycodes*, *Protopaleodictyon*, *Teichichnus*, and *Zoophycos*; as well as sporadic shafts.

The Gog Group is of Early Cambrian age, however, the paucity of index body fossils in these deposits has thwarted most attempts at precise age determinations. The presence of *Olenellus* Zone index fossils in the Peyto Member indicates that the Gog Group is Atdabanian in age at its youngest. The presence of well developed *Cruziana* and *Rusophycus* near the base of the Gog suggests that it is all of Atdabanian age.

These deposits contain a number of ichnotaxa that have been used as markers for the Cambrian-Ordovician boundary: *Cruziana furcifera*, *C. goldfussi*, *C. rugosa*, *Rusophycus rugosa*, and *Phycodes circinatum*. Their presence in the Gog Group indicates that, while these trace fossils may be useful as local or basin wide time markers, their stratigraphic distribution on a global scale is not sufficiently understood to use them as global index fossils. The same holds true for most trilobite generated ichnotaxa.

Part of the problem with trilobite produced ichnotaxa is the controversy over what features should be used to define these ichnotaxa. Many are defined on the basis of features which are presumed to reflect taxonomically significant anatomical features of the trace makers. This is a poor practice as there is no one-to-one relationship between trilobite biotaxa and ichnotaxa; anatomical features are inconsistently represented in the trace fossils; and the significance of many of these anatomical features, especially patterns of appendicular spines, to the systematics of trilobites is poorly understood. The taxonomy of these ichnofossils should be based on morphological features reflecting the behaviour, rather than the identity, of the trace makers.

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GLOSSARY

The following is a list of ichnological terms and other terms that are used in specific senses in this study that may differ from the sense in which they are used in other fields of study or in ordinary English. Formal stratigraphic names and units are used in accordance with the I.U.G.S. code of stratigraphic nomenclature, and all are capitalised.

Agrichnia: permanent dwelling traces related to farming or entrapment activities, usually comprising complex horizontal systems.

Boring: any structure cut into a lithified substrate.

Burrow: any structure, whether open, collapsed, or actively backfilled, emplaced in unlithified sediment, below the sediment surface.

Cubichnia: traces of resting and temporary shelter.

Domichnia: dwelling traces; the permanent domiciles of infaunal suspension-feeders, deposit-feeders, or carnivores.

Endichnia: trace fossils preserved in full relief within a layer of rock.

Endogene: a trace made within the sediment. (intrastratal emplacement=endogenic)

Epichnia: trace fossils preserved in concave or convex semirelief on the upper surface of a layer of rock.

Epifauna: animals that live on the sediment surface.

Ethology: the study of animal behaviour.

Exichnia: trace fossils preserved in full relief external to a layer of rock.

Exogene: a trace made on the sediment surface.

Facies: a label for a set of physical attributes that define a group of entities (rocks or strata). It is based solely on descriptive elements, including environment if this can be determined independently from physical appearance (only in active environments).

Fodinichnia: semipermanent dwelling and sediment processing traces.

Form: a term used in this study to denote an informal classification of trace fossils to account for local variations within an assemblage of trace fossils belonging to one ichnospecies. Forms are identified by a letter name, e.g. *Cruziana semiplicata* form A. This usage is of no relationship to that of Crimes (1970b, 1983) and Baldwin (1977a) which is provisional taxonomic rank, equivalent to ichnospecies.

Fossil: in this study, unless otherwise specified by the appropriate prefix, this term, and all its derivatives (fossiliferous ect.) refer to both body fossils and ichnofossils.

Fugichnia: escape structures resulting from rapid relocation within the sediment column.

Furrow: traces consisting of elongate troughs on the sediment surface, the result of a ploughing action combining digging and locomotion.

Hypichnia: trace fossils preserved in concave or convex semirelief on the lower surface of a layer of rock.

Ichnofacies: a label for a set of sedimentologic; lithologic; and ichnological attributes, expressed as the occurrence of certain types of traces or trace fossils, that define a group of rocks or strata. The relevant ichnological features are the gross form of the trace fossils: vertical cylinders, horizontal cylinders, horizontal ridges and grooves, and the presence of any linings or ornamentations as well as the relative and absolute abundances and spatial relationships.

Ichnofossil: a synonym of trace fossil.

Ichnogenus: the highest, formally accepted rank in the taxonomic classification of trace fossils (ichnotaxonomy).

Ichnology: the study of the effects of live animals on sediment, including biogenic sedimentary structures and fabrics.

Ichnospecies: the lowest, formally accepted rank in the taxonomic classification of trace fossils.

ichnosp.: on its own, this term identifies samples of a particular ichnogenus which could not, for reasons of exposure or preservation, be identified to the ichnospecific level, e.g. *Arenicolites* ichnosp. When "ichnosp." is accompanied by a number, e.g. ichnosp. 2, it identifies a group of samples of a particular ichnogenus which could not be correlated to a known ichnospecies but are sufficiently distinct that they probably represent a new ichnospecies.

Ichnotaxonomy: the taxonomic classification of trace fossils. Ichnotaxonomy is based on the morphology of trace fossils and is independent of their behavioural, preservational, or ecological classification.

Infauna: animals that live below the sediment surface.

Infill: any sediment that fills what would otherwise be an open trace. Passive infilling refers to sediment that settles into abandoned, open burrows by gravity. Active backfill refers to sediment that is actively packed into a burrow by the burrow producer as it moves through the sediment. When different sediment types or sediment and feces are alternated in dish like layers in the backfill, it is called meniscate backfill.

Interval: a term used in this study to denote a group of strata similar to a zone, but of a lower hierarchical rank.

Intergene: a trace made at the boundary between two sediment layers. (intrastratal emplacement=intergenic)

Pascichnia: grazing traces; a combination of feeding and locomotion whether exogenic, endogenic, or intergenic.

Repichnia: traces resulting from simple locomotion.

Scratch: traces or components of traces resulting from the intentional or unintentional sliding or scraping of a body part against the sediment. (=scratch mark)

Sequence: a term used in this study to denote a group of strata similar to a zone, but of a lower hierarchical rank than zone or interval.

Shaft: a vertical or predominantly vertical burrow or a vertical component of a larger burrow system.

Shape factor: the ratio of length divided by width in specimens of *Rusophycus*.

Spreite: a series of concentric arcs of sediment caused by incremental sifts in the position of a burrow. Spreiten that are between the last produce burrow and the sediment surface (or the burrow apertures in U-shaped burrows) are called protrusive. Spreiten below or distal to the last produced burrow are retrusive. (pl. spreiten)

Subunit: a term used in this study to denote an informal, arbitrary, continuous group of strata of lower rank than unit. Units and subunits form a hierarchical system so that units are the sum of their respective subunits. Subunits are defined on the basis of some unifying aspect of lithology or bedding style. They are used solely for the purpose of communicating the stratigraphic occurrence of ichnotaxa.

Trace: a mark or imprint left on the sediment by the activities of a living animal (=biogenic sedimentary structure).

Trace fossil: the preserved remains of a trace in the rock record (=ichnofossil).

Track: impressions and imprints of appendages made by living animals.

Trackway: traces composed of serial rows of tracks resulting from locomotion.

Trail: similar to trackways, but composed of more or less continuous marks or grooves, roughly parallel to the trend of motion, resulting from sliding or ploughing.

Tunnel: a burrow or boring that is maintained as an open structure for a permanent or semipermanent dwelling or food processing trace.

V-angle: the angle subtended by a V-mark.

V-mark: the V-shaped marks formed by oblique scratch marks on either side of a trackway or trail.

Unit: a term used in this study to denote an informal, arbitrary, continuous group of strata. Units are defined on the basis of dominant lithology and resistance to weathering. They are used as an aid to measuring section.

Zone: a term used in this study to denote an informal, continuous group of strata unified by some lithologic, sedimentary, or ichnological feature or features. Zones are used in the discussion of paleoenvironments and bear no necessary relationship to units or subunits.

INTRODUCTION

Purpose and Scope of Study

The purpose of this study was to make a comprehensive investigation of the ichnology of the Lower Cambrian Gog Group in the area of Lake Louise, Alberta. Observations were used to document the ichnological diversity of the region, to assess the ethological and ecological interpretation of certain ichnotaxa, especially those produced by trilobites, and to assess the local and global chronostratigraphic implications of the distribution of various stratigraphically important ichnogenera within the Gog Group. This study was also used as a focus for assessing the underlying concepts of ichnotaxonomy, especially for arthropod produced trace fossils, and how these concepts affect the utility of ichnotaxa for stratigraphy and environmental interpretation. Sedimentological data were collected to place ichnofossils within previously derived paleoenvironmental contexts. However, no major sedimentological or paleoenvironmental reinterpretations were made in this study.

The Gog Group is a thin, linear siliciclastic deposit extending along the Main Ranges of the Rocky Mountains of Alberta and British Columbia, Canada (figure 1). It consists of alternating zones of thickly bedded quartzites and thinly interbedded quartzites and pelites with minor carbonate lenses. The Gog Group was deposited along the western edge of the North American Craton during the Early Cambrian Period in a prograding shallow, shelf sea environment (figure 3). It is a deposit of intermediate character between the underlying, deep water slates and conglomerates of the Miette Group and the overlying Middle Cambrian, shallow water carbonates. The Gog Group in the study area of this report consists of intertidal flat, lagoon, and shallow subtidal deposits.

This study area was chosen because it has been the focus of previous work on regional mapping (Aitken, 1969; Palonen, 1976; Price *et al.*, 1980a, 1980b), regional paleogeographic reconstruction (Palonen,1976; see also Young, 1979), and detailed sedimentology (Palonen, 1976; Wolberg, 1986). However, there have been no previous comprehensive ichnological investigations in this area, and very few in the Lower Paleozoic deposits of the Cordillera in general.

Study Area

The study area is located within the Slate and Bow ranges of the Main Ranges in the Canadian Rocky Mountains. There are three collection sites, all within 15 km of the village of Lake Louise, Alberta (figure 1). Some minor collecting was also done around Lake Agnes, just west of Lake Louise. The entire study area is contained within map 82 N/8 of the National Topographic System. As all sites are within Banff and Yoho national parks, permission was obtained before travelling off marked paths and permits to collect samples were obtained.

Site 1 is the south face of Redoubt Mountain ($51^{o}27'$ N $116^{o}05'$ W, UTM grid reference 11U NH 633005). This is the site of the only measured section used in the study. It provides a 540 m thick, continuous section of the Gog Group extending from the basal, unconformable contact with the Precambrian Miette Group (plate 1c) through to the upper contact with the Middle Cambrian Mount Whyte Formation (plate 1a, b). Access was gained through several avalanche chutes where cover was minimal. North dipping beds provide good exposure of lower quartzite bedding surfaces. However, extensive bedding surfaces were not studied as no large blocks were found.

Site 2 is a talus cone off the northwest corner of Mount Babel, on the east shore of Moraine Lake ($51^{o}19'$ N $116^{o}11'$ W, UTM grid reference 11U NG 573857, figure 1). This site provides access to extensive bedding plane surfaces on large float pieces. All blocks appeared to be from the uppermost Fort Mountain Formation and above (figure 2), however, no precise stratigraphic positions could be ascertained.

Site 3 consists of several sites around Lake O'Hara, within the Lake O'Hara wilderness area ($51^{o}21$–$22'$ N $116^{o}19$–$20'$ W, UTM grid reference 11U NG 465–484 890–905, figure 1). Samples were collected from the avalanche chutes on Wiwaxy Peaks, the east and southeast shores of Lake O'Hara, and the plateau between Yukness Mountain and Mount Huber.

Previous Work

The eastern Canadian Cordillera of British Columbia and Alberta has been extensively investigated since the late nineteenth century (Palonen, 1976; Young, 1979; Wolberg, 1986). Most of this research has focused on local and regional sedimentology, stratigraphy, and later with regional correlation and paleogeographic interpretation and reconstruction (Palonen, 1976; Young, 1979). A detailed review of this work will not be included in this study as such reviews can be found in several other works (see Palonen, 1976; Young; 1979; and Wolberg, 1986).

Unlike the sedimentological and stratigraphical studies, however, there have been few comprehensive studies of the ichnology of these deposits. Most of the studies that have been made were concerned with the ichnology of the Precambrian-Cambrian boundary deposits (Fritz *et al.*, 1983; Aitken, 1984; Fritz and Crimes, 1985; Nowlan *et al.*, 1985) or with detailed discussions of specific taxa (Fenton and Fenton, 1937; Alpert, 1976). Three detailed studies have been made of the Lower Paleozoic ichnology of the Cordillera: Young, (1972) of the Gog and Cariboo groups in the Jasper region; Alpert, (1976) in the White-Inyo Mountains of California; and Fritz and Crimes (1985) of the Cassiar Mountains in the Yukon Territory (figure 1). No comprehensive study of the ichnology of the Lake

Louise area has ever been made.

Young (1972) described the ichnofossils of the Gog and Cariboo groups near Jasper, Alberta. The Gog Group in this area is composed of interbedded quartzite and shale zones and quartzite dominated zones similar to the Gog Group at Lake Louise (Young, 1972). The trace fossils at Jasper are similar to those at Lake Louise, however, the reported diversity of forms, at both the ichnogeneric and ichnospecific level, is much lower. Forms reported from Jasper are ?*Chondrites*, *Diplichnites*, *Planolites*, and *Rusophycus* (Young, 1972). *Didymaulichnus miettensis* is present in the Miette Group at Jasper (Young, 1972), but has not been reported at Lake Louise. No ichnofossils have been found in the Miette at Lake Louise (W. Arnott, pers. comm., 1987). The specimens of *Rusophycus* reported from the Gog in Jasper (Young, 1972) and the White-Inyo Mountains (Alpert, 1976) are identical to *Rusophycus* ichnosp. 3 and *R. eutendorfensis* from this study.

The trace fossils of the Precambrian-Cambrian boundary deposits from northern British Columbia and the Yukon have been studied by several authors (Fritz, 1980; Nowlan *et al.*, 1984; Fritz and Crimes, 1985). On average, these deposits are more shale dominated than the sandstone and quartzite dominated deposits of the Gog Group to the south, and are ascribed to deeper water environments. This paleoenvironmental difference is reflected in the trace fossils. A number of trace fossils common to the Gog Group are not found in the northern deposits. These include many permanent and semipermanent dwelling traces, most notably *Palaeophycus*, *Bergaueria*, *Dolopichnus*, and *Trichophycus* (Fritz and Crimes, 1985). The northern deposits contain a number of complex surface and shallow burrows not found in the Gog at Lake Louise, including *Helminthopsis*, *Neonerites*, and *Taphrehelminthopsis* (Fritz and Crimes, 1985). This can be attributed to the deeper, more quiet water environments of the northern deposits (Crimes and Anderson, 1985). Other trace fossils from these deposits that are not found in the Gog Group at Lake Louise are *Phycodes pedum*, *Plagiogmus*, and *Treptichnus* (Fritz and Crimes, 1985) which are common to Atdabanian and Tommotian deposits (see figure 28). Most trace fossils are similar to those in the Gog Group, including *Arenicolites*, *Chondrites*, *Cruziana*, *Didymaulichnus*, *Diplocraterion*, *Gordia*, *Monomorphichnus*, *Phycodes*, *Planolites*, *Skolithos*, *Teichichnus*, and *Rusophycus* (Fritz and Crimes, 1985). However, there is a much lower diversity, especially at the ichnospecific level, and especially among the trilobite traces which are also less well developed in terms of their depth and complexity of scratch mark pattern.

Regional Geology

The Gog and Miette groups, with their stratigraphic equivalents, form a thick, linear package of siliciclastic rocks along the eastern edge of the western Canadian Cordillera

(Young, 1972; figure 2). The Miette Group, the uppermost component of the Windermere Supergroup, consists of grey to maroon slates and greenish-grey, immature, feldspathic, coarse grained sandstone and conglomerate lenses (Young, 1972; Arnott, 1984). The Gog Group, the lowermost component of the Purcell Supergroup, unconformably overlies the Miette Group and consists of clean quartzite and interbedded quartzite and pelite (Young, 1972, 1979; Wolberg, 1986). This clastic package is overlain by Middle Cambrian carbonate deposits (Palonen, 1976; Young, 1979; Price *et al.*, 1980a, 1980b; Wolberg, 1986). The regional correlation and nomenclature of these deposits, and their lateral equivalents, is difficult because of a localised distribution of lithologic units; a wide variation in unit thickness and lithology; and an absence of time diagnostic fossils in most units (Wolberg, 1986). Regional correlation is based on regional mapping, lithologic similarity, and biostratigraphic control in the overlying Middle Cambrian units and in minor carbonate lenses within the Lower Cambrian deposits (Young, 1972, 1979; Palonen, 1976; Wolberg, 1986). Thus, while the upper boundary of this clastic package can be easily correlated, correlations within the clastic succession are difficult and uncertain (Palonen, 1976; Young, 1979). Figure 2 shows one generally accepted correlation of Lower Cambrian deposits in the eastern portion of the Cordillera.

The term Gog Group was first proposed by Deiss (1940) for the Lower Cambrian clastic deposits in the region around Lake Louise, Alberta (Palonen, 1976). The type section is at Mount Towers, by Gog Lake (Palonen, 1976). In the Lake Louise area, the Gog Group is divided into the Fort Mountain Formation, thick bedded quartzites and interbedded quartzite and pelite; the Lake Louise Formation, red and green shales and soft pink sandstones; the St. Pirian Formation, thick bedded quartzites and interbedded quartzite and pelite; and the Peyto Member, an arenaceous limestone (Wolberg, 1986). This nomenclature is used throughout most of the southeastern Rocky Mountains (Wolberg, 1986). The Middle Cambrian-Lower Cambrian boundary has been placed at the boundary between the Peyto Member and the overlying Mount Whyte Formation by the presence of olenellid trilobites in the Peyto Member and Middle Cambrian trilobites within the Mount Whyte (Rasetti, 1951; Wolberg, 1986).

The Gog Group in the Jasper region is divided into the McNaughton Formation, a quartzitic sandstone with minor shaly zones, the Mural Formation, limestone with red and green shales, the Mahto Formation, a quartzitic sandstone with frequent shaly intervals, and the Hota Formation, an arenaceous limestone (Young, 1972, 1979; Palonen, 1976; figure 4). The Middle Cambrian-Lower Cambrian boundary is placed at the contact between the Hota and the overlying Chetang Formation, based on paleontological evidence (Young, 1972). Correlation of the Gog Group with the Cariboo Group on the west side of the Rocky Mountain trench based on biostratigraphic and lithological correlation of the

Mural Formation in both areas (Young, 1972; figures 2 and 4). The Cariboo Group is a deep water lateral equivalent of the Gog Group (Young, 1972, 1979).

The Mural Formation in the Jasper area is correlated with the Lake Louise Formation in the Lake Louise area based on the lithologic similarity between the red and green shales (Palonen, 1986). Thus the McNaughton can be correlated to the Fort Mountain and the Mahto and Hota formations with the St. Pirian Formation and Peyto Member respectively (Wolberg, 1986; figure 2).

The contact between the Gog Group and the underlying Miette Group has been a source of much controversy (Wolberg, 1986). There is good evidence for a major unconformity between the Gog and the underlying Miette Group and Jasper Formation (Aitken, 1969; figure 2), however, the position of this boundary can be difficult to determine (Palonen, 1976; Wolberg, 1986). Part of the problem results from the stratigraphic contact between the basal, clean quartz pebble conglomeratic quartzite of the Gog Group and the Miette Group conglomerate lenses (Palonen, 1976). Where the basal conglomerate of the Gog Group rests directly on conglomerate lenses of the Miette Group, it can be difficult to distinguish the boundary. According to Palonen (1976) however, the Miette Group conglomerates can usually be distinguished by the dirty, feldspathic nature of the conglomerate matrix. At Lake Louise the unconformity has a small angular discontinuity, at Jasper it consists of a karsted disconformity and may be gradational in some places (Charlesworth *et al.*, 1967; Wolberg, 1986). Charlesworth *et al.* (1967) suggested, based on lithologic similarity, that the upper Precambrian Meadow Creek, Old Fort Point, and Wynd formations in the Jasper region are stratigraphically equivalent to the Corral Creek and Hector formations of the Miette Group in the Lake Louise area (figure 2). The Jasper Formation, a conglomeratic and feldspathic quartzite, was considered to be equivalent to the lower Fort Mountain at Lake Louise. Young (1979) also correlated it to westward extensions of the McNaughton. Palonen (1976) questioned this assessment of the Jasper since there were no feldspathic equivalents within the Fort Mountain. Either deposition of Jasper equivalents did not occur near Lake Louise or they were eroded away before deposition Fort Mountain Formation (Wolberg, 1986).

Near Field, British Columbia, west of Lake Louise, the Gog disappears beneath the Middle Cambrian Chancellor Formation. The basal Cambrian clastic succession reappears west of the Rocky Mountain Trench, in the Purcell, Selkirk, and Dogtooth mountains, where it forms the Hamill Group, Badshot Formation, and Lardeau Group (Wolberg, 1986; figure 2). These unconformably overly the Precambrian Horsethief Creek Group (Wolberg, 1986). The correlation of these units with the Gog Group is based on lithologic similarity and the presence of olenellid trilobites in the overlying carbonate units of both areas (Wolberg, 1986).

In the Cassiar Mountains, the late Proterozoic and early Paleozoic clastic strata are contained within the Rosella and Boya formations of the Atan Group and the Stelkuz and Espee formations of the Ingenika Group (Fritz, 1980a; figure 2). The Precambrian-Cambrian boundary is tentatively placed in the upper part of the Stelkuz Formation (Fritz, 1980b). Regional correlation with equivalent strata in the Jasper area suggests that the Rosella Formation is stratigraphically equivalent to the Mural, Mahto, and Hota while the Boya and upper Stelkuz are correlated to the McNaughton (Fritz, 1980a). In the Mackenzie Mountains, the Precambrian-Cambrian boundary is placed within the Vampire Formation based on trace fossil and small shelly fossil data (Fritz, 1980b; see Chapter 4, figure 2).

The lower Cambrian clastic succession (Gog Group) abruptly thins eastward in the subsurface of central Alberta (Wolberg, 1986). It is tentatively correlated with the "Basal Sandstone" unit of the Alberta Plain (Wolberg, 1986). This Basal Sandstone rests unconformably on the crystalline Canadian Shield and eventually pinches out against the Hudsonian basement (Wolberg, 1986).

Local Geology

The Bow valley-Lake Louise region is dominated by the Gog Group, which attains a maximum thickness of 1273 m (Wolberg, 1986). This clastic package rests on a major regional unconformity, eroded into the underlying non-fossiliferous feldspathic conglomerates and gritty maroon slates of the upper Windermere Supergroup with a slight angular discontinuity (Aitken, 1969; Palonen, 1976; plate 1c). The Gog Group is subdivided into four formations (Wolberg, 1986; figure 2). The Fort Mountain is composed of zones of thickly-bedded, cross-stratified quartzites with minor conglomerates and zones of thinly interbedded shale and quartzite (Palonen, 1976). The Lake Louise Formation consists of pale-green and maroon coloured, non-fossiliferous shale with minor quartz sandstones (Palonen, 1976). The wide range in thickness of this formation has prompted some workers to question its formational status (Wolberg, 1986). The St. Pirian Formation consists of cliff-forming, cross-stratified quartzite beds with zones of interbedded shale and quartzite (Palonen, 1976). The limestone Peyto Member contains abundant Olenellid Zone fauna (Walcott, 1890; Palonen, 1976) and ranges in thickness from 60 m to absent suggesting the presence of an erosional unconformity at the top of the Peyto Member (Palonen, 1976; Wolberg, 1986). The St Pirian Formation at Redoubt Mountain is directly overlain by the Middle Cambrian Mount Whyte, Cathedral, and Stephen formations (Walcott, 1890; Price *et al.*, 1980a, 1980b). The Mount Whyte and Stephen formations consist of grey-green interbedded shale, siltstone, limestone, and dolostone (Price *et al.*, 1980a, 1980b). The Cathedral Formation is composed of a massive, cliff forming limestone (Price *et al.*, 1980a, 1980b).

For the purposes of regional mapping, Palonen (1976) divided the Gog Group into seven informal units, alternating between resistant quartzite and recessive interbedded quartzite and pelite. The lower three units roughly correspond to the Fort Mountain Formation, unit four corresponds to the Lake Louise Formation, and the upper three units to the St. Pirian Formation. The Peyto Member does not form a part of this scheme. These units are easily distinguished in the field and correspond to major paleoenvironmental events (Palonen, 1976). These informal units, with slight modifications, form the basis of the stratigraphy used in this study (figure 16).

The study area is located within the Main Ranges of the Rocky Mountains, a region characterised by broad, open folds and flat, simple thrust faults controlled by the thick, competent Gog Group quartzites (Wolberg, 1986). These deposits are further cut by north trending, west dipping normal gravity faults (Wolberg, 1986). The dominant structural feature in the study area is the Simpson Pass Thrust Fault, the surface intersection of which is roughly coincident with the Bow River Valley (Price *et al.*, 1980a, 1980b; Hyws. 1 and 93 in figure 1). This fault separates the Redoubt Mountain section from the other collection sites used in the study. There must have been a considerable displacement along this fault since the Gog Group on the Lake Louise side of the fault is approximately twice as thick as it is on the Redoubt Mountain side (Price *et al.*, 1980a, 1980b). Thus, the original geographic separation between the Redoubt Mountain section and the supplementary collecting sites must have been much greater than at present.

Paleoenvironment of Deposition

The Gog Group forms part of a narrow, sinuous belt of late Proterozoic to early Paleozoic strata extending approximately 4000 km along the western edge of the North American Craton (Wolberg, 1986). The sediments confined within this linear trough setting are made up of non-volcanic, supracrustal rocks (Wolberg, 1986). This miogeoclinal setting thickens from regionally absent on the craton to several thousand metres thick over a distance of a few hundred kilometres to the west (Wolberg, 1986). This accumulation of coarse clastic sediments in the early Paleozoic Cordilleran miogeocline represents a westward thickening prism of shallow marine shelf to slope deposits (Palonen, 1976; Young, 1979; Wolberg, 1986). Thus, the Gog Group comprises the deposits of a shallow shelf sea along the edge of the North American Craton during the Early Cambrian (Palonen, 1976; Young, 1979). It forms a deposit of intermediate character between the underlying, deep water slates and conglomerates of the Miette Group and the overlying Middle Cambrian, stable, shallow water carbonates (Young, 1972, 1979).

The Miette and Gog groups have been interpreted as evidence for continental separation during the latest Precambrian or earliest Cambrian (see Arnott and Hein, 1986; Wolberg, 1986), with Miette and Gog sediments representing deposition along western trailing edge of the Cambrian passive continental margin during the post-rift phase of separation (Wolberg, 1986). The major stratigraphic hiatus separating the Gog and Miette is similar to breakup unconformities separating the syn-rift and post-rift sediments on modern continental margins (Wolberg, 1986). However, the contention that the Windermere and Purcell supergroups mark the initial sedimentation into a late Proterozoic, oceanic rift is contradicted by the lack of any indication of a western sediment source and the lack of oceanic crust underlying these deposits (Young, 1979).

The initiation of Gog Group sedimentation was the result of erosion off a newly formed, minor tectonic uplift along the western edge of the craton (Young, 1979). This sediment prograded out into a deep water basin dominated by mud and silt deposition and cut by gravel filled submarine canyons (Young, 1979; Arnott and Hein, 1986). Paleodispersal patterns, reflected in the prominent cross-bedding within the quartzites, indicate that Gog sediments were derived from the Precambrian Shield to the east and transported by southwest flowing currents (Palonen, 1976; Wolberg, 1986). Basin subsidence kept pace with sediment input, resulting in the accumulation of up to 3000 m of sediment (Young, 1979). The basal conglomeratic quartzites in eastern deposits of the Gog Group represent the initial surge of coarse detritus from the newly formed uplands (Young, 1979).

The Gog Group is dominated by arenaceous rocks with cross-bedding indicating current action and trace fossils indicative of near shore marine biotopes (Palonen, 1976). Thus, the dominant environment of deposition was that of a shallow marine shelf sea, marginal to the craton (Young, 1972, 1979; Palonen, 1976; Wolberg, 1986). There are however, a large number of environments represented in these deposits, ranging from alluvial plains and deltas to bathyal settings (Young, 1972). The abundance of quartz pebbles, mixed altered and unaltered feldspars, and the drab colour and chemical maturity of the quartzites indicate a source area with considerable topographic relief and a warm, humid, nonseasonal climate (Young, 1979).

The influence of tidal processes on Gog group sedimentation appears to have been much greater than that of catastrophic processes (Wolberg, 1986). Paleogeographic reconstructions from Scotese *et al.* (1979) place the study area just north of the equator during the early Cambrian, a latitude which should have been in a zone frequented by tropical hurricanes and winter storms given patterns of atmospheric circulation similar to the present (Wolberg, 1986; figure 3). The minor influence of catastrophic meteorological events on Gog Group sedimentation is assumed to reflect: the paleogeographic location of the study area in the north central lee of Laurentia, sheltered from low latitude hurricane tracks; stronger early Cambrian tides resulting from a smaller distance between the moon to the earth; the absence of polar ice caps at this time, which would have reduced the polar-equatorial temperature gradient, thus reducing storm nucleation; and the continuous subsidence and sediment supply which favoured the preservation of day-to-day sedimentary processes (Young, 1979; Wolberg, 1986). Evidence for tidal influence consists of: bimodal and trimodal distributions of cross-bedding orientations; the presence of sand waves, dunes, and ripples within size ranges characteristic of modern tidal flats; thin sand waves; bimodal distribution of cross-bedding angles indicating constructional and destructional bed form migration; excellent sorting and rounding of grains within deposits related to individual environments; interbedding of autochthonous carbonates and clastics; mud cracks in shales interbedded with sand dunes; and the presence trace fossils indicative of both the *Skolithos* and *Cruziana* ichnofacies (Palonen, 1976).

Local Paleoenvironment

The Gog Group at Lake Louise was deposited in an intertidal flat to shallow subtidal environment (Palonen, 1976). The alternating recessive and resistant units of the Gog Group in the Lake Louise area represent changes in the position of the paleoshoreline (Palonen, 1976; figure 16). The resistant units are dominated by sandy, upper tidal flat deposits with migrating tidal channels; along with minor swash zone and tide pool deposits (Palonen, 1976). The first and third recessive units are shallow subtidal deposits while the second recessive unit represents a lagoon environment (Palonen, 1976). Regional correlation of the shaly units with quartzite dominated units to the north, south, and east suggests that the Lake Louise area comprised a large embayment during the deposition of the Gog Group (Palonen, 1976).

Shoreline deposits are rare in the southern Canadian Rockies, however, the Gog Group thins in the subsurface near Banff suggesting a possible position of the paleoshoreline (Wolberg, 1986). There is no evidence of alluvial deposits in the Lake Louise area (Palonen, 1976). The Gog quartzites are much thinner at Redoubt Mountain than at the other sites (Price *et al.*, 1980a, 1980b) suggesting that it was closer to the margin of the depositional basin. There is no evidence for turbidity flows in the study area indicating that it was wholly on the continental shelf (Wolberg, 1976). Ichnological and sedimentological evidence supports a shallow, fully marine depositional environment (Palonen, 1976; Wolberg, 1986).

Introduction to Ichnology

Ichnology is the study of sedimentary structures produced by the activities of living plants and animals (Häntzschel, 1975; Ekdale *et al.*, 1984). Traces, a subset of biogenic sedimentary structures, include tracks; trackways; trails; burrows; borings; miscellaneous bioerosion structures including drill holes and bite marks; feces and pseudofeces ranging from large lumps and small pellets to continuous strings; and structures produced by the purposeful actions of plants, such as rooting (Ekdale *et al.*, 1984; see Glossary). The terms trace and trace fossil are usually confined to distinct structures and thus do not include features such as stromatolites, biogenic graded bedding, and biogenic mottling of sediment, although these are still biogenic sedimentary structures (Pemberton and Frey, 1982; Ekdale *et al.*, 1984). Structures produced as integral elements of the producer's anatomy, such as egg shells, agglutinated foram tests, and worm tubes, are not considered traces as they do not reflect any particular activity on the part of the organism (Ekdale *et al.*, 1984). For the same reason, body moulds, casts, and marks produced by the movement of dead organisms are also not considered traces (Ekdale *et al.*, 1984).

Once the substrate in which a trace is emplaced becomes lithified, the trace becomes a trace fossil, also called an ichnofossil. The successful preservation of a trace requires that two other criteria be met. First, a trace must be produced or infilled in such a way as to make it visible as a fossil. In simple, open burrows this occurs by casting with sediment of a different composition than the substrate of emplacement, producing lithologic discontinuities (Baldwin, 1977a; Ekdale *et al.*, 1984). The construction of distinct features like linings or pellets can render a trace fossil visible in the absence of lithologic discontinuities but infilling must still occur to prevent collapse of open burrows (Häntzschel, 1975; Ekdale *et al.*, 1984). In actively backfilled traces, the modification of sediment lithology or structure in the infill, through ingestion, sorting, or alternating layers of feces and rejected sediment, can produce subtle lithologic differences between the burrow infill and the surrounding rock (Pemberton and Frey, 1982). Traces must also be protected from destruction by further biogenic and physical reworking prior to lithification (Häntzschel, 1975; Ekdale *et al.*, 1984). This occurs through infilling of open structures and by rapid burial to a depth below the active layer of sediment, where biogenic and physical modification of the sediment takes place (Häntzschel, 1975; Ekdale *et al.*, 1984).

One problem with the recognition of trace fossils is the differentiation of biogenic sedimentary structures from physical sedimentary structures (Ekdale *et al.*, 1984). This can be a confusing matter, and often relies as much on personal experience and prejudice as on objective criteria (Ekdale *et al.*, 1984). Some of the common features of trace fossils that can be used to this end are: a resemblance to an anatomical feature of a potential trace maker; uniform dimensions and/or continuity of structures; uniform size in multiple structures; lack of current alignment; regular and complex patterns; linings and distinct walls; spreiten; meniscate infill; pellets; organic residue; very delicate features; preservation in full relief; and association with body fossils (Ekdale *et al.*, 1984). It must be noted however, that exceptions to all these correlations exist in both biogenic and physical sedimentary structures (Ekdale *et al.*, 1984).

History of Ichnology

Although certain trace fossils (mostly vertebrate tracks) have been recognised as the result of the activities of animals since the eighteenth century, an organised approach to ichnology and universal recognition of these structures as the result of animal behaviour did not come about until the 1930's and 1940's (Osgood, 1970; Häntzschel, 1975; Ekdale *et al.*, 1984). Osgood (1970) recognised three phases in the development of ichnology.

In the first phase, *circa* 1820 to 1873, many of these structures were named and described, however, most were interpreted as fossilised algae and soft bodied vermiform animals rather than biogenic sedimentary structures. The majority were provisionally lumped under the informal category of "fucoids", reflecting their supposed algal affiliation, or labelled *incertae sedis* (Osgood, 1970; Häntzschel, 1975). After 1850, some invertebrate trace fossils, as well as an increasing number of vertebrate trace fossils, began to be described and given formal names as biogenic sedimentary structures, however, most continued to be described as plant body fossils.

Osgood's (1970) second phase in the development of ichnology began in the early 1870's with the first serious challenges to the anatomical interpretation of fucoids. The principle works were those of J. Hall, J.F. James, and especially A.G. Nathorst (see Häntzschel, 1975). Nathorst, concentrating on the fucoids *Cruziana* and *Rusophycus*, effectively refuted the botanical explanation of their formation by observing modern tracks and burrows; experimenting with their production and preservation; and noting the similarities between preserved modern traces and fucoids. He also noted that organic residues were never found in these structures and that many *Cruziana* and *Rusophycus* had a much greater relief than would be expected in a plant that was impressed into the sediment under its own weight. However, although these works effectively refuted the fucoid interpretation, the debate between the proponents the body fossil and trace fossil origin of these structures lasted for the rest of the 1800's (Osgood, 1970).

After the turn of the century, the trace fossil interpretation of "fucoids" was firmly established (Häntzschel, 1975). Interest in these structures waned considerably at this point, primarily because the significance of trace fossils was not appreciated (Ekdale *et al.*, 1984). However, after the 1930's, research into the environmental significance of modern traces sparked renewed interest in ichnology as a tool in paleoecological and paleoenvironmental analyses (Häntzschel, 1975; Ekdale *et al.*, 1984).

Classification of Ichnofossils

There are four primary modes of classification for ichnofossils: formational; preservational; ethological; and taxonomic (Chamberlain, 1971; Häntzschel, 1975; Ekdale *et al.*, 1984). Formational classification distinguishes trace fossils based on the interpreted mode of emplacement of the original trace. It recognises three basic categories: exogenic traces, formed at the sediment-water interface; endogenic traces, emplaced within the sediment; and intergenic traces, formed at the boundary between different sediment layers (Häntzschel, 1975). There are several different strategies for the preservational classification of ichnofossils (Ekdale *et al.*, 1984). Seilacher's (1964) strategy distinguishes between trace fossils preserved in full relief within beds; in semirelief on upper or lower bedding surfaces; or in cleavage relief where traces are expressed as distorted sediment laminae a small distance below the surface of emplacement (Ekdale *et al.*, 1984). Martinsson's (1970) strategy classifies the preservation of trace fossils based on their spatial relationship to the resistant sediment that actually preserves the trace, usually sandstone. Full relief trace fossils cast in sandstone are termed exichnia; full relief trace fossils moulded in sandstone are termed endichnia; and semirelief trace fossils are termed epichnia and hypichnia for trace fossils occurring on the upper and lower surfaces of sandstones respectively (Ekdale *et al.*, 1984). The terms cast and moulded are used in a descriptive sense only, to describe the topological relationship between the trace and the sandstone. Figure 5 shows these various forms of preservation. It is important to note that the mode of formation of a trace bears no necessary relationship to the mode of preservation of the resulting trace fossil and that traces produced in any of the three modes of emplacement can be preserved in any of the above modes of preservation (Ekdale *et al.*, 1984).

Trace fossils can also be classified according to the interpreted ethology of the original trace (Ekdale *et al.*, 1984). There are seven basic categories to this classification: *agrichnia*, permanent and semipermanent, complex detritus and microfaunal entrapment structures (see *Protopaleodictyon*); *cubichnia*, temporary resting traces (some *Rusophycus*); *domichnia*, permanent to semipermanent dwelling structures (*Skolithos*); *fodinichnia*, deposit-feeding burrows (*Phycodes*); *fugichnia*, escape structures, usually vertical relocation of a burrow following sudden deposition of sediment; *pascichnia*, grazing traces that combine continuous locomotion and feeding; and *repichnia*, locomotion traces (some *Cruziana*) (Ekdale *et al.*, 1984).

Ichnotaxonomy

Trace fossil taxonomy is a descriptive classification of ichnofossils based on morphology (Häntzschel, 1975; Ekdale *et al.*, 1984). A system of formal nomenclature forms an integral part of this classification (Ekdale *et al.*, 1984). Formal nomenclature is important because it is the means by which ichnotaxa are communicated, permitting accurate communication without lengthy descriptions or inaccurate labels, and it insures that ichnotaxa will not be lost in the literature (Osgood, 1970; Ekdale *et al.*, 1984). There are two separate systems in the taxonomy of trace fossils, ichnotaxonomy which is a classification based on behaviour, and biotaxonomy which is based on the inferred trace maker, whether in an absolute or relative sense (Osgood, 1970; Chamberlain, 1971; Pemberton and Frey, 1982; Ekdale *et al.*, 1984; see Chapter 4).

Ichnotaxonomy is based on morphological features which are interpreted to be behaviourally significant (Fürsich, 1974a, 1974b; Ekdale *et al.*, 1984). This behavioural emphasis is based on the mechanics and physical results of behaviour rather than the purpose or function of the behaviour, as in ethological classification, since one morphological type of trace can result from a number of different activities. As an example, *Rusophycus* can be produced by resting, feeding, physical protection and several other activities without any appreciable difference in the physical appearance of the trace (see Ichnogenus *Rusophycus*). Moreover, some trace fossils can pass through different uses with time. *Thalassinoides*, for example, start out as a feeding structures and are later modified into dwelling burrows (Bromley and Frey, 1974).

Differences in trace fossil morphology reflecting preservation effects and non-functional anatomical features of the trace maker are not to be included in ichnotaxonomy (Fürsich, 1974a; Ekdale *et al.*, 1984; Gureyev, 1985). However, differences in trace morphology resulting from the same activity performed in different substrates are used in ichnotaxonomy (Bromley and Frey, 1974; Ekdale *et al.*, 1984) as the conditions under which an action is performed is a significant aspect of behaviour. Functional anatomical features of the trace maker, related to the production of the trace, are often used in ichnotaxonomy as well, since such features are an integral part of the mechanics of behaviour of the trace maker (Gould, 1982; Gureyev, 1985; see Chapter 4). Non-fossilised traces are not treated under ichnotaxonomy, only trace fossils (Pemberton and Frey, 1982).

Ichnotaxonomy is a hierarchical system with two levels, ichnogenus and ichnospecies, although there are some informal higher ranks (Pemberton and Frey, 1982; Ekdale *et al.*, 1984). There is no underlying phylogenetic basis to this classification, ichnospecies are not necessarily related genetically to other ichnospecies within an ichnogenus (Ekdale *et al.*, 1984; Gureyev, 1985).

Biotaxonomy is a classification of trace fossils by inferred trace maker and is, thus, based on morphological features that provide clues to the identity of the trace maker (Ekdale *et al.*, 1984). Ichnotaxonomy and biotaxonomy are totally separate systems, as exemplified by the following four points. The same species of trace maker may produce more than one kind of biogenic structure as a result of different behavioural patterns, either in response to different environmental influences or as components of a behavioural repertoire of different day-to-day activities (Osgood, 1970; Chamberlain, 1971; Pemberton and Frey, 1982; Ekdale *et al.*, 1984). For example, trilobites produced *Cruziana, Dimorphichnus, Diplichnites, Monomorphichnus, Protichnites*, and *Rusophycus* under the same physical conditions as the result of different physiological requirements (Crimes, 1970c). The same species of trace maker can produce different biogenic structures using the same behaviour in different substrates or at different positions relative to lithologic interfaces (Ekdale *et al.*, 1984). The same ichnotaxon can be produced by a number of distinct species of trace makers, especially forms such as *Skolithos* which have a simple construction that does not reflect the anatomy of the trace maker (Osgood, 1970; Chamberlain, 1971; Pemberton and Frey, 1982; Ekdale *et al.*, 1984). As a result, trace fossils typically have long time ranges, sometimes spanning the entire Phanerozoic (Ekdale *et al.*, 1984). A single trace fossil can be produced and/or inhabited by more than one species of animal either simultaneously or in succession (Ekdale *et al.*, 1984). Another distinctive feature of ichnotaxonomy is that different ichnotaxa, which in most cases exist as distinct taxa, can grade into each other within a single specimen (Crimes 1970c; Bromley and Frey, 1974; Osgood and Drennen, 1975; Bergström, 1976; Pemberton and Frey, 1982; Pickerill *et al.*, 1984). Trace fossils may also represent the cumulative activity of an animal over time and not reflect the active burrow configuration at any one time (Bromley and Frey, 1974). The significance and ichnotaxonomic problems of this phenomenon is discussed in detail in Chapter 4.

Thus, there is no correlation between the concepts of ichnotaxonomy and biotaxonomy (Ekdale *et al.*, 1984). Moreover, ichnotaxonomy is not just a temporary system employed because the identity of trace makers can not be determined or are not yet determined, both are necessary and both provide useful information (Pemberton and Frey, 1982; Ekdale *et al.*, 1984). A corollary to this is that ichnotaxonomic diversity and biotaxonomic diversity can not be correlated, since a given benthic community can produce different traces and a different number of traces under different circumstances and different benthic communities can produce similar assemblages of traces under certain conditions (Ekdale *et al.*, 1984). The relationship between ichnotaxonomy and biotaxonomy is still a source of confusion and controversy however (Ekdale *et al.*, 1984), and is discussed in more detail in Chapter 3 under ichnogenus *Cruziana* and in Chapter 4.

Applications of Ichnology

Trace fossils have applications ranging from structural geology, sedimentology, paleoecology, and environmental reconstruction (see Häntzschel, 1975; Ekdale *et al.*, 1984). One of the principle uses of trace fossils is in paleoenvironmental reconstruction and as indicators of certain specific environmental conditions (Ekdale *et al.*, 1984). Trace fossils are intrinsically suited to this purpose since animal behaviour is a direct response to environmental stimuli (Gould, 1982). Trace fossils are often indicative of a certain set of physical and ecological conditions (Ekdale *et al.*, 1984), such as *Chondrites*, which is indicative of deep buried, organic rich, dysoxic sediment (Bromley and Ekdale, 1984), or *Skolithos*, which is indicative of high water energy and suspended organics (Goodwin and Anderson, 1974). Thus, assemblages of trace fossils, in conjunction with sedimentary features, are very useful in reconstructing past environments (Ekdale *et al.*, 1984). Ichnofossils have several advantages over body fossils in this respect. Unlike body fossils, they are always found *in situ* (Ekdale *et al.*, 1984). As well, the number of viable behavioural patterns in a given environment is small whereas the types of animals performing these behaviours can vary considerably in different occurrences of the same environmental conditions. Thus behaviour patterns are often better at characterising environments and certain environmental conditions than the specific animals present. This concept is best expressed in the classification of recurrent ichnofacies (Seilacher, 1967; Ekdale *et al.*, 1984). Ichnofacies are naturally recurrent associations of behavioural patterns expressed as naturally recurrent assemblages of trace fossils types, shafts or mixed surface trails and horizontal burrows for example, rather than specific ichnotaxa (Seilacher, 1967; Crimes, 1975c; Ekdale *et al.*, 1984). Ichnofacies are indicative of certain environmental conditions such as oxygenation or sediment consistency but are not necessarily indicative of any particular, large scale environment (Ekdale *et al.*, 1984). Another advantage that trace fossils have for environmental reconstruction is that they are typically well preserved in environments where body fossils have a low potential for preservation, most notably siliciclastic dominated environments (Bergström, 1973; Ekdale *et al.*, 1984; Seilacher, 1985).

Trace fossils can also be used to indirectly study the trace making organisms themselves, especially their ecology and general behaviour. They are most useful, in this respect, for trace makers which have no modern analogues, such as trilobites; trace makers that have a low fossilisation potential, such as animals without well mineralised skeletons; and in environments in which the preservation potential of body fossils in general is low, such as sand dominated environments (Crimes, 1970c; Ekdale *et al.*, 1984; Seilacher, 1985). Trace fossils can also be used to study the ecology and evolution of behaviour in general sense (Seilacher, 1974, 1977b; Ekdale *et al.*, 1984). Another important application of ichnofossils is in biostratigraphy and its application to chronostratigraphy (Seilacher, 1970; Crimes, 1975c; Ekdale *et al.*, 1984). In this respect, they can be used both as behavioural entities and as indicators of certain trace makers. This topic is discussed at length in Chapter 4.

Investigative Methods

The Redoubt Mountain section, site 1, was the primary site in this study. Ichnological data were collected along with stratigraphic and sedimentary/environmental data. The other sites were used primarily to study large bedding surfaces and to get a better estimate of the diversity of ichnofossils over the whole study area. Samples were not collected according to any pattern, except that at Redoubt Mountain they were collected from within a 10-30 m wide strip within the avalanche chute. The abundance of different ichnotaxa at Redoubt Mountain was estimated subjectively. Attempts to correlate samples from the supplementary collecting sites to precise stratigraphic intervals at Redoubt Mountain were deemed to be impractical due to poor access to section and the substantial difference in thickness between the Redoubt Mountain section and the sections from these sites. Rough approximations could sometimes be made however, based on lithologic similarities. Ichnological data from all sites were collected as photographs and samples. Notes were made of ichnofossil descriptions and of the stratigraphic and sedimentological context of all samples and photographs. Sedimentological observations were recorded in photographs and written descriptions.

The Redoubt Mountain section was divided into seven alternating recessive and cliff forming resistant units similar to those of Palonen (1976). Unit seven was not included in this study due to lack of time and poor weather. Each of these units was further divided into subunits corresponding to intervals of similar lithology. Although associations of trace fossils with sedimentary features both within and between subunits were noted and are discussed for paleoenvironmental and ecological interpretations, stratigraphic occurrences of ichnotaxa are recorded with reference to entire subunits. The reason for this is that the large size and low density of most ichnotaxa makes it difficult to estimate their true local stratigraphic range. As the genesis and preservation of trace fossils is strongly controlled by sedimentary facies and environment (Ekdale *et al.*, 1984) their stratigraphic ranges are far more likely to correspond to major changes in lithology than measured first or last occurrences of particular specimens in section.

SYSTEMATIC ICHNOLOGY

Ichnotaxa are organised alphabetically by ichnogenus and ichnospecies. Ichnogenus discussions are of a general scope, while ichnospecies discussions and descriptions are concerned as much with the particular samples. Known stratigraphic ranges are given for all ichnogenera as well as some key ichnospecies. These do not include the data from this study so that occurrences from this study can be easily compared to the previously known ranges. Partial synonymies lists are given for some ichnotaxa. These are not meant to be comprehensive lists, rather they are lists of other ichnotaxa that, although still in common use, are, or are likely to be, junior synonyms of the ichnotaxon in question.

Ichnogenus *Arenicolites* Salter, 1857

Type Ichnospecies

Arenicolites carbonaria Binney, 1852, by subsequent designation of Richter, 1924

Diagnosis

Simple U-shaped tubes without spreite, perpendicular to bedding. Walls are usually smooth, although lining and sculpturing may be present. Absolute and relative dimensions are not diagnostic. Tube arms may be unequal in diameter. (after Häntzschel, 1975; Chamberlain, 1977)

Stratigraphic Range

Arenicolites is known from deposits of the late Precambrian to the Recent (Chamberlain, 1977; Crimes and Anderson, 1985).

Discussion

Arenicolites is interpreted to be the infilled remains of open, U-shaped burrows that had free connection to the surface at both ends (Osgood, 1970). They are distinguished from other U-shaped shafts by the lack of well developed branching or spreiten (Häntzschel, 1975).

Arenicolites burrows may be lined or non-lined. The presence of a distinct burrow lining indicates noncohesive sediment or unsuitable sediment pore water chemistry (Goodwin and Anderson, 1974). Burrow depth is at least partly dependent on trace maker anatomy. Exceptionally deep burrows however, are indicative of either periodic emergence or an erosionally unstable substrate (Goodwin and Anderson, 1974). The lack of spreiten indicates that the trace maker was incapable of adjusting its burrow depth or that the precise burrow depth was not of critical importance to the trace maker.

U-shaped burrows form the dwelling and feeding burrows of a large number of extant filter-feeding and surface deposit-feeding invertebrates, most commonly polychaetes, insects, and crustaceans (Chamberlain, 1977; Eagar *et al.*, 1985). Surface deposit-feeders utilising such a burrow require at least periodic quiet water conditions that allow settling out of organics and periodic high energy conditions, supplying a quantity of organic material that is sufficient to allow regular reforaging of a small area around the burrow. Filter-feeders utilising such a burrow set up a one way current through the tube, filtering out food particles on a mucus trap or specialised body parts. This strategy requires strong enough currents to suspend organic particles in the water column.

The presence of U-shaped rather than straight shafts is probably as much an artifact of the identity of the trace maker as it is a function environmental constraints. However, the use of U-shaped burrows for filter-feeding may have slightly different optimal conditions compared to the use of vertical burrows and fan-shaped filters held up in the water column. An abundance of predatory organisms within the water column, weak currents, where food particles move close to or along the bottom, or strong turbulence would lower the efficiency of exposed, fan-like filters compared to U shaped burrow systems. Stronger currents where food particles are kept up, away from the sediment surface may reverse this relative efficiency. U-shaped burrows allow for more efficient water flow through the burrow. This may facilitate the maintenance of suitable living conditions within dysoxic environments.

Arenicolites is most commonly found in deposits attributed to shallow marine environments (Fillion and Pickerill, 1984) although it is also found in deposits of fresh water (Bromley and Asgaard, 1979), tidal flat, and deep marine environments (Crimes *et al.*, 1977).

Differentiation between *Arenicolites*, *Diplocraterion*, and *Skolithos* can be difficult when identification is made from bedding plane exposures (Osgood, 1970). *Diplocraterion* may not always have spreiten extending all the way up the arms of the tube. Thus both *Arenicolites* and *Diplocraterion* may be exposed on bedding planes as simple paired tubes with no interconnecting spreiten. On the other hand, there are cases where the tube arms of *Arenicolites* may be connected by a bar-like structure at the surface. This is caused by sediment sagging between the tube arms after death or departure of the causative organism (Osgood, 1970). In such cases the sediment laminae can still be traced between the arms in side section (Osgood, 1970). In the absence of interconnecting bars, either of these two ichnogenera may be mistaken for *Skolithos* in pipe rock or on other densely bioturbated surfaces where the pairing of tubes is not obvious (Osgood, 1970).

Arenicolites ichnosp.
plate 12f

Occurrence

Specimens of *Arenicolites* ichnosp. were observed in only one bed, comprising subunit 4b. A number of specimens of uncertain affinity were identified throughout units 2 and 6.

Description

Specimens from subunit 4b were observed in side section within a clean trough cross-bedded quartzite. They consist of smooth walled, quartzite infilled, U-shaped burrows. Some burrows appear to have a thin weathered-out zone separating them from the host rock suggesting the presence of a thin lining. The burrow diameter varies from 1–2 mm, while the inner separation of the burrow arms is 5–15 mm. Burrow depth averages 150 mm with well rounded bases. Upper burrow terminations occur at several reactivation surfaces within the bed, thus the burrow tops may not have been preserved. There is no evidence of any change in cross-sectional morphology along the burrow length. Burrow distribution along the exposed face is uneven, with separations varying from 10 mm to greater than 100 mm.

A number of specimens were tentatively identified on bedding planes in thinly interbedded quartzites and shale. They consist of paired vertical tubes, unlined and with a quartzite infill. Burrow diameters and separations vary considerably from occurrence to occurrence, ranging from 1–7 mm and 5–30 mm respectively. Burrows occur in clusters of 3–10 pairs over areas of 100–400 square centimetres. The presence of spreiten could not be ascertained.

Discussion

The specimens from subunit 4b are definitely *Arenicolites*. The high current strength, indicated by the clean, sandy substrate and trough cross-bedding, suggests an environment favouring filter-feeders. The possibility that the burrows were lined is consistent with a clean sand substrate which would not have supported open tubes. There is no evidence for readjustment of burrow depth in any of the specimens, indicating that the burrows had their extreme depth while in use. This probably reflects periodic emergence, an erosionally unstable sediment, or a combination of both. The number of reactivation surfaces within the rock is indicative of a high frequency of erosional events. The protection from erosion and emergence afforded by the extreme burrow depth (Goodwin and Anderson, 1974) would offset the difficulty in constructing, maintaining, and circulating water through such a long, narrow tube.

This form closely resembles Chamberlain's (1977) diagnosis of *Arenicolites sparsus* Salter, 1857. The ratio of width over depth is less than half that of Chamberlain's diagnosis however, and the presence of any funnelling at the apertures could not be verified in these samples.

The paired shafts in units 2 and 6 are presumed to be *Arenicolites*, although the presence of U shaped burrows or spreiten was never verified.

Ichnogenus *Astropolichnus* Crimes and Anderson, 1985

Type Ichnospecies

Astropolichnus hispanicus Crimes *et al.*, 1977, by subsequent designation of Crimes and Anderson, 1985

Diagnosis

Cylindrical to subcylindrical, vertical burrows bearing numerous non-branched radial ridges and narrow groves, surrounding a central axial cylinder. Diameter is greater than or equal to the height (Pemberton *et al.*, 1988).

Stratigraphic Range

Astropolichnus is an early Cambrian trace fossil, having been found in deposits of Tommotian and Atdabanian age (Crimes, 1987).

Discussion

Astropolichnus consists of shallow, cylindrical burrows with diameters roughly 3 times the height (Pemberton *et al.*, 1988). The lower surface is covered with non-branched radial ridges and narrow grooves surrounding a central, roughly cylindrical axial stalk (Pemberton *et al.*, 1988). It is usually preserved as convex hypichnia infilled with coarser material than the surrounding rock (Pemberton *et al.*, 1988).

Astropolichnus is interpreted to be a coelenterate burrow, similar to *Bergaueria* (Crimes and Anderson, 1985). The central cylinder is the result of a basal stalk, possibly retractable, which may have served to anchor the trace maker and facilitate its movement within the burrow (Crimes *et al.*, 1977). *Astropolichnus* is thought to represent a resting and feeding burrow (Pemberton *et al.*, 1988) and is probably indicative of similar environmental conditions to *Bergaueria* and *Dolopichnus*.

Astropolichnus was erected for those ichnospecies of *Astropolithon* that are of biogenic origin after it was determined that the type ichnospecies of *Astropolithon* (*A. hindii*) was the result of fluidized sand volcanoes (Crimes and Anderson, 1985). It can be distinguished from *Bergaueria* by the central stalk and from *Dolopichnus* by the well developed radial ridges and large diameter to height ratio (Pemberton *et al.*, 1988).

Astropolichnus ichnosp.

Diagnosis

Cylindrical burrows consisting of a raised rim in epirelief, having numerous non-branched radial ridges surrounding a circular, central axial cylinder (Pemberton *et al.*, 1988).

Occurrence

A single specimen of *Astropolichnus* ichnosp. was found on float at Moraine Lake.

Description

The specimen consists of a 65 mm diameter, 7 mm high cylindrical mound with a 20 mm diameter, 5 mm deep central depression. It is preserved on the base of a 4 cm thick quartzite bed with abundant *Phycodes* ichnosp. *Planolites montanus* and *Rusophycus bilobatum*.

Discussion

This specimen is quite poorly preserved and abraded. Although at present, *Astropolichnus hispanicus* is the only recognised ichnospecies of this ichnogenus (Pemberton *et al.*, 1988), insufficient detail is preserved in this specimen to make more than an ichnogeneric assignment.

Ichnogenus *Bergaueria* Prantl, 1946

Type Ichnospecies

Bergaueria perata Prantl, 1945

Diagnosis

Cylindrical to hemispherical, vertical to subvertical burrows with smooth, unornamented, rarely lined walls; circular to elliptical cross-sections; and essentially structureless infill. The base is flat to rounded and may have radial ridges; a central depression; and concentric impressions. (Pemberton *et al.*, 1988)

Stratigraphic Range

Bergaueria is known from the uppermost Precambrian to the Pleistocene (Pemberton *et al.*, 1988), although is is most common in the lower Paleozoic (Alpert, 1973; Pemberton *et al.*, 1988).

Discussion

Bergaueria consists of lined or unlined, smooth walled cylindrical to hemispherical mounds with structureless infill (Pemberton *et al.*, 1988). Apical ornamentation may be present and varies from central and concentric depressions to radially arranged protuberances (Pemberton *et al.*, 1988). Burrow diameters are commonly greater than or equal to the depth (Pemberton *et al.*, 1988).

Bergaueria is most often found on the basal sandstone bedding surfaces, with an infill identical to the overlying rock (Alpert, 1973; Pemberton *et al.*, 1988). It occurs as isolated structures, in small groups of well spaced structures, and in large dense clusters with non intersecting individuals (Alpert, 1973; Pemberton *et al.*, 1988). The latter habit is most common in the Lower Cambrian (S.G. Pemberton, pers. comm., 1988). The absence of intersecting individuals suggests that density of burrows is the actual density of live individuals. Similar densities of epifaunal, soft sediment dwelling anemones have been observed on modern tidal flats (S. Speyer, pers. comm., 1988).

Bergaueria is interpreted to be the cast of permanent or semipermanent dwelling burrows made by actinarian sea anemones (Alpert, 1973). Supporting evidence comes from the matching radial symmetry in the surface features of the trace fossils and modern actinarians and the production of similar traces by modern actinarians (Alpert, 1973; Boardman *et al.*, 1987).

An alternate interpretation is that *Bergaueria* represents a resting pit (Häntzschel, 1975; Hakes, 1976). However, given the rather sedate life habits of sea anemones and and the amount of trouble and time it takes for them to dig these pits (Barnes, 1980), this does not seem to be a plausible interpretation. As well, modern burrowing anemones use their burrows as dwellings (Barnes, 1980). Another problem with this interpretation is the existence of dense clusters of *Bergaueria*. It seems unlikely that large numbers of anemones would create temporary resting pits at the same time and place. The same argument can be used to refute the hypothesis that lined *Bergaueria* are more permanent dwellings than unlined ones. It is more likely that the presence of burrow linings reflect the presence of low sediment consistency or unsuitable pore water chemistry (see Goodwin and Anderson, 1974).

The most common mode of preservation is thought to have been rapid burial resulting in death of the trace maker *in situ* and the slumping of the overlying sediment into the burrow as the animal decomposed (Alpert, 1973). This hypothesis is supported by the presence of slump structures both within the burrow cast and in the overlying sediment (Alpert, 1973). Observations on dense clusters of *Bergaueria* observed in this study support this hypothesis. Individual burrow casts are often separated by layers of shaly sediment less than 5 mm thick but with no evident disruption of the shape of the burrow wall. This would not be expected if the animal crawled out of the burrow or if the burrow was empty when infilled.

Sea anemones combine filter-feeding and carnivorous feeding strategies. Food is captured from the water column and the surrounding sediment surface and varies from large detritus particles to plankton, fish, and crustaceans (Barnes, 1980). Burrows sometimes have a lining of shell fragments (Alpert and Moore, 1975). This probably results from the contents of the coelenteron being packed against the burrow sides as trace maker's corpse decays. This indicates that some *Bergaueria* trace makers were predatory (Alpert and Moore, 1975). Thus, unlike true filter-feeders, *Bergaueria* trace makers do not necessarily require sufficient water agitation to suspend organic detritus.

Bergaueria is only rarely found in vertical stacks (Pemberton *et al.*, 1988). This indicates that in most cases, the trace makers did not readjust their burrows in response to heavy sedimentation. *Bergaueria* also lack basal protrusions indicative of a physa (an anchoring organ, Pemberton *et al.*, 1988) thus the trace makers may not have been able to easily adjust themselves within the burrow or dig new burrows as adults. *Bergaueria* must therefore, be indicative of conditions of low sedimentation and stable substrates.

Modern sea anemones inhabit near normal marine environments (Boardman *et al.*, 1987). However, on tidal flats burrowing anemones can tolerate daily drops in salinity of over 10 permil below normal marine conditions. Burrowing anemones range from the arctic to the tropics (Boardman *et al.*, 1987; personal observation) and from intertidal flats (personal observation) to abyssal depths (Heezen and Hollister, 1971). *Bergaueria* is most commonly associated with shallow marine deposits (Crimes *et al.*, 1977) but has been found in rocks attributed to lagoon, tidal flat, and shoreface environments (Miller and Knox, 1985), brackish environments (Hakes, 1985), and bathyal environments (Eagar *et al.*, 1985; Ksiazkiewicz, 1977).

Ichnospecific differentiation in *Bergaueria* is based on apical ornamentation as well as the presence of distinct wall linings (Alpert, 1973; Pemberton *et al.*, 1988). Alpert (1973) claims that the variation in apical ornamentation is caused by the final state of contraction of the muscles when the animal dies. Three of the ichnospecies of *Bergaueria* could have resulted from the three possible states of muscle contraction: longitudinal muscles contracted (see *B. radiata*); circumferential muscles contracted (see *B. perata*); and both sets relaxed (see *B. hemispherica*) (Alpert, 1973). However, it is hard to explain large dense clusters of the same ichnospecies of *Bergaueria* by this mechanism. It is unlikely that such a large number of anemones would die at the same time with their apical muscles in the same state of contraction. Thus, these differences must also be due, in part, to taxonomic differences in the trace makers. In either case it is difficult to apply any environmental significance to occurrences of these three ichnospecies.

Bergaueria hemispherica Crimes *et al.*, 1977
plates 6f; 7a, b, c

Diagnosis

Bergaueria with thinly lined walls and a flat to rounded, smooth apical surfaces (Pemberton *et al.*, 1988).

Occurrence

Specimens of *Bergaueria hemispherica* were found in subunits 4s and 6a as well as on float at Moraine Lake and Lake O'Hara.

Description

Specimens consist of cylindrical to hemispherical burrows preserved as hypichnia on quartzite beds, overlying brown shales. Burrows are quartzite infilled and unlined. Apical surfaces are smooth and slightly rounded to hemispherical. Burrow diameter varies from 5–50 mm and is 1–3.5 times the height. Although there is a large overall range in diameter, individuals in one group seldom vary by more than 15 mm. On one float block however, there are two distinct size classes averaging 35 mm and 7 mm in diameter (plate 7c). Specimens occur as isolated structures or in clusters of close packed individuals separated by 0–20 mm. These clusters often cover more than 2000 square centimetres and contain up to 100 individuals (plate 7a). However, all clusters are seen as fragments and thus, their true extent can not be assessed. Most specimens, including all those within dense clusters, are straight and vertical. There are several isolated specimens that are tilted at approximately 45° to bedding (plate 7b). In these cases, all but one side of the burrow is vertical.

Discussion

Bergaueria hemispherica is distinguished by a lack of apical features (Pemberton *et al.*, 1988).

The mean diameter to height ratio of the specimens in this study is close to 2, the value given in Pemberton *et al.* (1988). This ratio is quite variable, both within and between groups of burrows however. This indicates that either height and width of the original burrows varied independently, burrows were irregularly truncated during burial, or irregularly compressed after burial. Truncation is unlikely given Alpert's (1973) mode of preservation. The fact that in large clusters of *Bergaueria*, diameter varied much more than the height, on an apparently flat surface, favours the first explanation.

A small number of burrows are hemispherical rather than cylindrical. This is probably due to collapse of the burrow walls during burial since the burrow walls are much smoother and less sharply defined than those of cylindrical specimens. Tilted burrows are common, especially around the edges of dense clusters. Burrow walls are sharp with well defined fine detail, thus these burrows probably represent animals living at an angle within the sediment rather than burrow collapse.

Dense clusters of *B. hemispherica* are common. Non-intersecting burrows and similar quality of preservation between individuals indicate that these burrows were all occupied at the time of burial. Thus, large expanses of live anemones, separated by less than a centimetre must have been common in this area. Similar densities of burrowing anemones can be seen on modern intertidal flats (S. Speyer, pers. comm., 1988). The sample with two size classes of *Bergaueria* may have resulted from the presence of two different taxa of trace maker or two distinct age classes of the same taxon.

Bergaueria perata Prantl, 1945

plate 6a, b, c, e

Diagnosis

Bergaueria with smooth, unornamented walls and a flat to rounded base which may have faint radial ridges; one or more central depressions; and concentric circular impressions (Pemberton *et al.*, 1988).

Occurence

Bergaueria perata was found in subunits 2b, 2s, and 4o as well as on float at Moraine Lake and Lake O'Hara.

Description

Specimens consist of cylindrical to hemispherical burrows preserved as hypichnia on quartzite beds, overlying brown shales. Burrows are quartzite infilled and unlined. Apical surfaces are flat to slightly rounded. Apical ornamentation varies from a 5–10 mm wide, 1–3 mm deep central depression or protuberance (plate 6e); 1–5 mm wide, 1–2 mm deep, concentrically arranged circular grooves (plate 6a, f); to faint, 1–2 mm wide, closely spaced radial ridges (plate 6d). Burrow diameter varies from 17–55 mm and is 1–4.6 times the height. Although there is a large overall range in diameter, individuals in one group seldom vary by more than 15 mm.

Specimens occur as isolated structures or in clusters of close packed individuals separated by 5–300 mm. Most specimens are straight and vertical although there are several isolated specimens that are tilted at approximately 30^0 to bedding (plate 6b). In these cases, all but one side of the burrow is vertical. These specimens are more cone shaped and have concentric rings down the sides of the trace.

Discussion

Bergaueria perata is distinguished by a central depression and may have a number of concentric depressions and radial ridges (Pemberton *et al.*, 1988). The radial ridges differ from those on *B. radiata* in that they are fine, faint, and numerous (plate 6c). *Bergaueria perata* occurs as isolated hemispherical mounds and in dense clusters similar to *B. hemispherica.*

B. perata occurs as tilted burrows, however, these are more conical in shape than the straight specimens and have distinct circumferential ridges down the side of the trace. Tilted forms of *B. perata* never occur with straight forms as do tilted forms of *B. hemispherica*. The distinct shape and lack of association suggests that tilted forms of *Bergaueria perata* were probably produced by a different trace maker than the straight forms. The tilted forms resemble *Bergaueria prantli* Ksiazkiewicz, 1977, however, Pemberton *et al.* (1988) synonymised *B. prantli* with *B. perata.*

One example of *Bergaueria perata* was found with a sandstone and shale laminated infill in zone 3 of unit 4. Given the high current energies postulated for this zone it is more likely that this burrow represents gradual upward migration in response to sediment accumulation, similar to Crimes *et al.* (1977), than passive infilling of an abandoned burrow.

Bergaueria radiata Alpert, 1973

plate 6d, f

Diagnosis

Bergaueria with distinct, prominent radial ridges around a single, apical, concentric depression (Pemberton *et al.*, 1988).

Occurrence

A single specimen of *Bergaueria radiata* was found on float at Lake O'Hara.

Description

The specimen consists of a cylindrical burrow, preserved as a hypichnia on a thin quartzite bed, overlying a brown shale. The burrow is quartzite infilled and unlined. The apical surface has a 12 mm diameter 2–3 mm thick apical disk with a 5 mm wide central depression and vague 1–2 mm long, well spaced radial ridges. The burrow diameter is 35 mm and is approximately 1.5 times the height. The specimen occurs on a small block, in a small close spaced cluster consisting of a specimen of *Bergaueria perata* and *B. hemispherica.*

Discussion

Bergaueria radiata is distinguished by its large, central apical disk with wide, short, strongly impressed radial ridges (Pemberton *et al.*, 1988). This sample is unique in that it contains three different ichnospecies of *Bergaueria* in one small cluster. This indicates that different types of anemones lived in very close proximity to each other, as is seen in modern anemones.

Ichnogenus *Chondrites* von Sternberg, 1833

Type Ichnospecies

Fucoides antiquus Brongniart, 1882, by subsequent designation of Andrews, 1955

Diagnosis

A system of ramifying tunnels consisting of one or more proximal, near vertical main tubes which branch out into distal tunnels, more parallel to bedding. Tunnels are unlined with sharply defined walls and maintain a roughly constant diameter within tunnel systems. Branching may be pinnate, radial, or grouped. Interpenetration is rare within tunnel systems. (after Osgood, 1970; Häntzschel, 1975; Chamberlain, 1977)

Stratigraphic Range

Chondrites is known from Cambrian to Recent deposits (Osgood, 1970; Häntzschel, 1975; Bromley and Ekdale, 1984).

Discussion

The structure of *Chondrites* consists of one or more central shafts that give way to a system of ramifying tunnels that generally curve distally towards the horizontal. The pattern of branching and the spacing between branches, laterally and along length, are quite variable between specimens. There may be several orders of branching within a system. The tunnels are of roughly constant diameter within a system. They are unlined but sharply defined against the host rock. The infill is structureless and generally similar to the host rock. The longest known *Chondrites* tunnel approaches 40 cm long, the known range in burrow diameter is 0.5–5 mm. (after Osgood, 1970)

The interpretation of *Chondrites* is dealt with at length in Osgood (1970). It is one of the most controversial traces and one of the last of the "fucoids" to be widely accepted as a trace fossil. Previous interpretations have ranged from algae, plant roots, sponges, and brood chambers. Although many of these hypotheses still have adherents, the most widely accepted interpretation is that *Chondrites* is a feeding structure produced by infaunal deposit-feeders (Osgood, 1970).

Chondrites are fossilised tunnel systems which had free connection to the surface and were left open after abandonment (Osgood, 1970; Bromley and Ekdale, 1984). It is thought to have been made by repeated probing and withdrawal of the trace maker either by moving through the sediment (Osgood, 1970; Bromley and Ekdale, 1984) or from a point near the surface using an extensible proboscis (Osgood, 1970). Although the fossil tunnels are unlined, it is likely that a thin mucus lining was present in the original burrow (Osgood, 1970). Such a lining would facilitate movement of the organism and prevent the collapse of the tunnel after departure of the trace maker. Thin mucus linings have a poor preservation potential however, unless they can adsorb a sediment which contrasts with the lithology of the burrow infill and surrounding sediment (see Ichnogenus *Skolithos*).

The mode of preservation of *Chondrites* is still a matter of controversy (Osgood, 1970). The most widely accepted hypothesis is that the tunnel systems were passively infilled after abandonment (Osgood, 1970). After conducting test on mechanical models of the trace and detailed examination of the infill of actual samples Osgood (1970) claimed that this is a plausible, and in some cases probable explanation.

The list of proposed trace makers for *Chondrites* is extensive, ranging from nematodes (Bromley and Ekdale, 1984); sipunculids; enteropneusts; annelids (Osgood, 1970); and small arthropods (A.A. Ekdale, pers. comm., 1988). Sipunculids, enteropneusts, and some annelids are capable of extending certain body parts to lengths in excess of the longest known *Chondrites* (Osgood, 1970) and could have probed down into the sediment from a fixed point near the surface. Arthropods and other small trace makers would have moved through the sediment while excavating the burrow system and maintained a free connection to the surface. This mode of formation is favoured by some ichnologists (A.A. Ekdale, pers. comm., 1988) as no modern analogue for the former process has been observed.

Chondrites is not indicative of any particular environment. It is found in substrates ranging from shale and mudstone to sandstone, and occurs in both siliciclastic and carbonate deposits (Bromley and Ekdale, 1984). It is indicative of firm to stiff sediment (Ekdale *et al.*, 1984), especially as it is often emplaced at a considerable depth below the sediment surface (Osgood, 1970). It has been found in rocks attributed to environments ranging from marginal marine settings (Hakes, 1985), tidal flats (Ekdale *et al.*, 1984), shallow subtidal environments (Fillion and Pickerill, 1984), shallow shelf seas (Vossler and Pemberton, 1988), and abyssal deposits (Bromley and Ekdale, 1984).

The primary control on the occurrence of *Chondrites* is the level of oxygenation within the interstitial waters of the sediment (Bromley and Ekdale, 1984). It is a behaviour pattern that is adapted to exploit deeply buried, dysoxic and/or organic rich layers (Bromley and Ekdale, 1984; Vossler and Pemberton, 1988). Open connection with the water column allows for the maintenance of sufficiently oxygenated conditions in the burrow although the surrounding sediment may be depleted in oxygen.

Dysoxic sediment layers near the surface result when organic rich sediment is buried below a sediment with low permeability, or when the water column becomes oxygen depleted. In this situation, *Chondrites* is often the only trace fossil present, as the environment can not support animals intolerant dysaerobic conditions (Bromley and Ekdale, 1984). The *Chondrites* behaviour is also adapted for exploiting sediments that have been made dysoxic at depth. In this case *Chondrites* is the last trace emplaced and cross-cuts other burrows made when the the strata were closer to the surface. In this situation, *Chondrites* often selectively burrows into previous burrow linings (Bromley and Frey, 1974; Bromley and Ekdale 1984). *Chondrites* is often found on the base of thick sandstone beds. Events which deposit thick sand layers can bury surface detritus below the level in which other deposit-feeders work and often result in the development of local dysoxic conditions. *Chondrites* trace makers are often the only animals to utilise such deposits (Ekdale *et al.*, 1984).

The classification of *Chondrites* at the ichnospecific level is difficult due to the large number of synonymous and often poorly defined ichnospecies (Osgood, 1970;

Chamberlain, 1977; Fillion and Pickerill, 1984; S.G. Pemberton, pers. comm., 1988). As a result, the specimens in this study are not classified to the ichnospecific level, rather a set of informal groupings, based on branching patterns and burrow geometry, is used, similar to the strategy used by Osgood (1970). The branching pattern in *Chondrites* is probably controlled primarily by the identity of the trace maker with little environmental influence. The overall geometry of the burrow system, however, is probably most strongly influenced by the geometry of the organic rich sediment body being utilised, whether a thin layer or thick region.

Chondrites form A
plate 8f

Occurrence

Chondrites form A was found at one horizon in subunit 2k and on several float blocks from Moraine Lake.

Description

Specimens consist of irregularly straight to curving, unlined, clean quartzite infilled, horizontal burrows, 3 mm in diameter. Burrows exhibit up to two orders of dichotomous branching, with branching angles from 40–80° and segment lengths from 5–20 mm. Tunnels are not spaced close together and the tunnel systems, as a whole, spread out both vertically and horizontally. Tunnels are preserved as hypichnia within thin, grey to orange shales on the base of thick quartzite beds.

Discussion

The irregular geometry of this form closely resembles *Chondrites* type A of Osgood (1970, text figure 10, p. 335). However, the tunnel diameter is approximately 6 times larger than Osgood's material, indicating production by a different trace maker. *Chondrites* form A does not seem to have been adapted for the efficient utilisation of a volume of sediment as are more regularly patterned forms of *Chondrites*.

Chondrites form B
plate 8a, d, c

Occurrence

Chondrites form B occurs sporadically throughout unit 2, subunits 4n to 4y, and subunits 6a, 6c, and 6d. It was positively identified in 10 samples and tentatively identified in 16 others.

Description

Specimens consist of straight to slightly curving, unlined, clean quartzite infilled, dichotomously branching, horizontal burrows, 1–3 mm in diameter. The length of segments, whether isolated or between branches, varies from 5–15 mm. The lateral spacing between burrows varies from 3–8 mm.

The burrows are preserved as hypichnia within thin, dark to black shales on the base of clean quartzite beds and within thinly interbedded quartzites and dark shales. One specimen occurs as a burrow along the periphery of a large *Teichichnus* in subunit 6d (plate 8a).

Discussion

Chondrites form B is similar to *Chondrites* type B of Osgood (1970), however poor exposure of the tunnel patterns inhibits a confident comparison. *Chondrites* form B frequently occurs in highly bioturbated, interbedded shales and thin quartzites which contain abundant *Planolites montanus* of a similar diameter to the *Chondrites*. Thus, some occurrences of *Chondrites* may have been overlooked, especially where the *Chondrites* is exposed as short, isolated burrows. Recognition of this form was, in many cases, made on the basis of the geometric relationships between short burrow segments without seeing actual branching (plate 8d). Frequent nonrecognition of *Chondrites* might result in an underestimation of the development of dysoxic or anoxic conditions within the sediment.

In some instances, such as when *Chondrites* selectively burrows other burrows for example (plate 8a), *Chondrites* is the last burrow to have been emplaced in the sample. This is typical for *Chondrites*, as it is a behaviour adapted to utilising deeply buried sediments, below the level of other bioturbating organisms (Bromley and Ekdale, 1984). In many samples from this however, *Chondrites* are cross-cut by other horizontal burrows and complex feeding traces such as *Phycodes*. This suggests that this ecological tiering shown in Bromley and Ekdale (1984) might not have been as well developed in the early Paleozoic. The occurrence of *Chondrites* along the periphery of other burrows reflects the concentration of organic material as feces in the infill (Bromley and Frey, 1974). Once taken up by bacteria, this material becomes a suitable food source for the *Chondrites* trace maker.

Chondrites form C
plates 7b, c; 8c

Occurrence

Chondrites form C was found in subunit 2b and on large float blocks at Moraine Lake.

Description

Specimens consist of straight to gently curving, unlined, clean quartzite infilled burrows, 3–5 mm in diameter. There are two branching styles: dichotomous and pinnate, often found within the same burrow system. The pinnate branches are 1–2 mm narrower than the main burrow. This may however, be due to a vertical shift of the branches with respect to the plane of exposure. Pinnate branching angles vary from 30–80^{o}, while the dichotomous branching angles vary from 10–40^{o}. Burrow length between branches varies from 10–50 mm.

Chondrites form C is preserved as hypichnia within brown and orange shales on the base of thick, cross-bedded quartzites. It often occurs as dense, overcrossing mats of burrows. Interpenetration is rare. These densely burrowed horizons frequently occur in the open spaces within dense clusters of *Bergaueria* (plate 7a, c).

Discussion

This form of *Chondrites* is distinguished from form B in that it forms a distinct size class of burrow. It also, on average, tends to be preserved below much thicker quartzite beds. This suggests that the difference between these two forms results from a different traced maker, the larger of which (making *C.* form C) could burrow through deeper sand layers. The *Chondrites* found within the *Bergaueria* clusters are a response to the presence of organic material produced by the decomposition of the *Bergaueria* trace makers. The depth of burial and development of dysoxic conditions must have excluded most other deposit- feeders.

Chondrites form D
plate 8b

Occurrence

Chondrites form D was found in subunits 2b, 2j, 2k, 2o, 4m, and 6c as well as on float at Lake O'Hara.

Description

Specimens consist of gently curved, unlined, quartzite infilled tubes, 5 mm in diameter and, on average, up to 15 mm long. Side branches project off the main tube at low angles and curve around to follow the main tube with separations of 0–5 mm. This results in a pinnate pattern of branching. Specimens were preserved as hypichnia on thin quartzite beds within dark coloured shales.

Discussion

This form resembles *Buthrotrephis palmatum* as discussed in Osgood (1970). The relationship between *Chondrites* and *Phycodes* (*Buthrotrephis*) *palmatum* is discussed below under *Phycodes palmatum*. *Chondrites* form D is also similar to *Phycodes pedum* Seilacher, 1955 but the branches of *Chondrites* form D are longer and do not form the feather-stitch pattern seen in *Phycodes pedum*. *Chondrites* form D resembles *Phycodes palmatum*, from this study, except for a lack of spreiten and a branching pattern that is pinnate and two dimensional rather than the three dimensional bundles seen in *Phycodes*. The consistent difference in branching style suggests that the lack of spreiten is not due to poor preservation.

Ichnogenus *Cochlichnus* Hitchcock, 1858

Type Ichnospecies

Cochlichnus anguineus Hitchcock, 1858

Diagnosis

Regular and smoothly meandering burrows, resembling sine curves (Häntzschel, 1975).

Stratigraphic Range

Cochlichnus is known from Vendian to Tertiary deposits (Webby, 1970; Häntzschel, 1975; Crimes, 1987).

Discussion

Cochlichnus consists of smooth, sine-wave shaped linear features. It is interpreted to be the repichnia or pascichnia of vermiform animals (Eagar *et al.*, 1985). Both surface trails (Webby, 1970; Eagar *et al.*, 1985) and burrows (Crimes *et al.*, 1977) appear to have been included within this ichnogenus. The diagnostic feature, which both have in common, is the overall sinusoidal shape of the structure. This was probably the result of a form of motion in which the propulsive force was exerted against the curves in the trail or burrow, similar to the type of movement employed by snakes. This strategy would be necessary where substrate consistency is insufficient for peristaltic or appendage mediated propulsion or for trace makers that lack the required musculature or body parts to implement these other strategies (Hakes, 1976; Runnegar, 1982). *Cochlichnus* differs from *Beloraphe* in that the latter has angular, rather than smooth, bends (Häntzschel, 1975). This angularity is inconsistent with the type of locomotion proposed for *Cochlichnus*.

Cochlichnus has been found in rocks from a wide range of environments: deep sea flysch deposits (Ksiazkiewicz, 1977); deltaic settings from delta top to distal turbidites (Eagar *et al.*, 1985); shallow subtidal sand and mud flats (Crimes *et al.*, 1977); intertidal deposits (Narbonne, 1984); and channel fill, point bar, flood plain, and lacustrine deposits (Archer and Maples, 1984). It does not necessarily imply fully marine conditions (Hakes, 1976).

Cochlichnus ichnosp.
plate 10f

Occurrence

Cochlichnus ichnosp. was found in subunit 4s and on float at Lake O'Hara

Description

Specimens consist of 3–5 mm diameter, unlined, silty quartzite infilled burrows that exhibit a regular horizontal zig-zag pattern consisting of smooth but abrupt, alternating left and right handed, 90° turns at regular intervals of 10–20 mm. Burrows are preserved as convex hypichnia on the base of thin quartzite and siltstone beds within thinly interlaminated shales and quartzites.

Discussion

The samples collected in this study appeared to be true burrows rather than trails. However, the high degree of compaction and thinly interlaminated nature of the rocks makes this a tenuous interpretation at best. The differentiation of ichnospecies within the ichnogenus *Cochlichnus* is in a somewhat confused state. The only apparent morphological groupings within it are those of true burrows and trails. Since these two distinctions are inconsistently applied to different ichnospecies in the literature (see Webby, 1970; Pickerill, 1981) no attempt was made in this study to identify the specimens beyond the ichnogeneric level.

Ichnogenus *Cruziana* d'Orbigny, 1842

=*Bilobites* d'Orbigny, 1839 (*Partim*) (Osgood, 1970)
?=*Crossopodia* M'Coy, 1851 (Bergström, 1973)
?=*Rouaultia* de Tromelin, 1877 (Bergström, 1973)
?=*Crossochorda* Schimper, 1879 (Osgood, 1970; Bergström, 1973)
=*Isopodichnus* Bornemann, 1889 (Bromley and Asgaard, 1979)

Type Ichnospecies

Cruziana rugosa d'Orbigny, 1842, by subsequent designation of Miller, 1889

Diagnosis

Elongate furrows bisected by a median gap or groove. This may be bounded on either side by an outer lobe and/or thin marginal ridges which always occur along the outer edge of the trace. The surfaces of the lobes are covered with scratch-like striations, usually at an angle to the trend of the furrow. (after Häntzschel, 1975)

Stratigraphic Range

Cruziana has been reported from early Cambrian to Jurassic deposits although it is best known from deposits of Cambrian to Devonian age (Crimes, 1970b; Häntzschel, 1975; Bromley and Asgaard, 1979; Pienkowski, 1985).

Discussion

Morphology

Cruziana is an elongate furrow consisting of a median groove bordered by one or more lobes and thin ridges (Crimes, 1970c). It is almost always preserved as a positive relief, hypichnial cast on the basal bedding surface of sandstone or siltstone beds overlying shales or siltstones (Crimes, 1970c; Goldring, 1985). The complexity and variability of this ichnogenus makes a general description difficult to formulate. The following is condensed from Crimes (1970c), Seilacher (1970), and Häntzschel (1975) (figures 8, 9).

The *Cruziana* band is divided by a medial depression that varies from a narrow groove to a distinct, thin gap. This is flanked by one or two pairs of band-like lobes. The cross-sectional shape of the lobes varies from flat to well rounded. Where there are two sets of lobes, there may be a distinct break or a smooth gradation between the medial and lateral lobes. Thin marginal ridges may be present and these may be continuous or discontinuous and contain one or more elements. Both the medial and lateral lobes are usually covered with scratch-like marks. In most cases, the scratch marks on the medial lobes are distinct, coarse, made up of 1–4 tightly spaced elements, that pass transversely to obliquely across the lobes. There are two other patterns of scratch marking found on medial lobes: those in which the scratch marks consist of up to 6–12 elements that fan out towards the outer edge of the lobe (see *Rusophycus avalonensis*) and those in which the scratch marks are roughly parallel and near longitudinal (see *C. furcifera*, *C. goldfussi*, *C. rugosa*, and *Rusophycus rugosa*). The lateral lobes, where present, are usually covered with fine, often wispy lineations varying from oblique to longitudinal. In most cases, the above features are symmetrical across the median groove. Furrows may vary considerably along length with respect to any of the above features.

Interpretation

As with many traces fossils, *Cruziana* was originally interpreted as a "fucoid", the remains of marine algae, and was one of the last ichnogenera to be universally accepted as a trace fossil (see Osgood, 1970 and Häntzschel, 1975 for a review of the history of this ichnogenus).

Cruziana is now interpreted to be the result of trilobites and other arthropods furrowing within the sediment, either along the sediment surface (Crimes, 1975b; Baldwin, 1977b; figure 9) or along a lithologic discontinuity within the sediment (Goldring, 1985; Seilacher, 1985). This combination of locomotion and sediment excavation results in a continuous trough. The furrow is either immediately infilled by collapse of the overlying sand behind the trace maker, in the case of intrastratal formation, or infilled by sand deposition at a later time in the case of surface emplacement. It is the cast which forms the resulting trace fossil (figure 8).

Trace Makers

Most Paleozoic *Cruziana* are assumed to have been made by trilobites (Seilacher, 1970), although direct evidence for this is almost entirely lacking (Bergström, 1973; Seilacher, 1985). The lack of direct evidence is to be expected however, since these trace fossils are best preserved in moderate to high energy, siliciclastic settings, where the preservation potential of body fossils is negligible (Bergström, 1973; Seilacher, 1985). There is however, contrary to Whittington (1980), some direct evidence and a wealth of indirect evidence that supports a trilobite origin for most *Cruziana*. The best evidence comes from *Rusophycus* (see *Rusophycus*). The common association and intergradation of *Cruziana* and *Diplichnites* with *Rusophycus* indicates a similar group of trace makers for all three ichnogenera. As well, the stratigraphic ranges of trilobites and *Cruziana* mirror each other with respect to abundance, diversity, average size, and maximum sizes (Bergström, 1973; Ekdale *et al.*, 1984; Seilacher, 1985). Thus, one can confidently claim that most *Cruziana* were made by trilobites. However, almost any arthropod group is capable of producing *Cruziana* and *Rusophycus* (Bergström, 1973) and there are several ichnospecies of *Cruziana* that, on the basis of size, impressions of body parts, or stratigraphic context, are likely to have been produced by branchiopods; limulids; and a number of unknown arthropod groups other than trilobites (Seilacher, 1970, 1985; Bergström, 1973).

Mechanics of Formation

The mechanics of formation for *Cruziana* have only been rigorously studied with respect to trilobites. An understanding of the appendicular morphology of trilobites is crucial to the understanding of their traces, however their appendage structure is poorly known and from only a few trilobite taxa (Bergström, 1973; Whittington, 1980; Seilacher, 1985; Müller and Walossek, 1987; figures 6, 7). The appendages of trilobites consist of two branches, an inner telopodite and an outer exite (see Bergström, 1972, figure 2; Whittington, 1980, text figure 8; Müller and Walossek, 1987; figure 6). The telopodite, is a simple multijointed appendage with spines and setae along the limb as well as at the end (Bergström, 1972; Whittington, 1980; Müller and Walossek, 1987; figures 6, 7, 8). The exite is composed of a flat plate of spines or filaments attached to a jointed or unjointed base (Bergström, 1972; Whittington, 1980; Müller and Walossek, 1987; figures 6, 7, 8). Both the telopodite and exite are attached at the proximal end to a coxa which attaches to the ventral body surface (Whittington, 1980; Müller and Walossek, 1987; figure 6).

By reason of morphological similarity, the coarse medial lobe scratch marks of *Cruziana* are interpreted as having been made by the telopodites (Crimes, 1970c, 1975a, 1975b; Seilacher, 1970; Bergström, 1973). The inferred motion is that of a postero-medial directed digging stroke proceeding in waves of motion from the back to the front of the trilobite (Osgood, 1970; figure 8). This results in V-shaped scratch marks that open in the direction of travel (Crimes, 1970c; figures 8, 9). Independent evidence for the direction of travel comes from functional morphological analyses of appendage construction (Whittington, 1980; Whittington and Almond, 1987); cross-cutting relationships where scratch marks are cross-cut by others on the open side of the V-mark (Häntzschel, 1975); and intergradation with *Rusophycus* and *Diplichnites*, both of which have independent indicators of forward direction. It should not be assumed, however, that V-marks must open forward in all cases, especially where a trilobite origin is questionable (Osgood, 1970;

Bergström, 1976). Many instances of non-trilobite produced *Diplichnites* and limulid produced *Cruziana* have V-marks that open back rather than forward (Osgood, 1970; Seilacher, 1985).

Lateral lobes are found in a small number of *Cruziana* (Seilacher, 1970). In most cases they are assumed to have been made by dragging the exite branches (Seilacher, 1970; Bergström, 1973; Crimes, 1975b; figure 8) however, in some forms both medial and lateral lobes may have been made by the telopodites (Crimes, 1975a; see *C. semiplicata*). Marginal ridges are interpreted to be the result of genal spines dragging along the sediment (Crimes, 1970c, 1975a; Seilacher, 1970) or the dragging of the edges of the pleurae (Seilacher, 1970) although Crimes (1975a) considered the latter process unlikely.

The postero-medial motion of the telopodites across the medial lobes is assumed by most ichnologists (Crimes, 1970c, 1975a, 1975b; Seilacher, 1970) to have provided both the digging action and the propulsive force involved in *Cruziana* (figure 10). Many aspects of trilobite locomotion can be deduced from their trace fossils. Crimes (1970c) noted several features of *Cruziana semiplicata* that can be used to deduce the speed of movement (figure 9). The ratio of the scratch mark width relative to the total body width can be deduced since the marginal ridges provide a constant index of body width (Crimes, 1970c). Smaller ratios indicate a shorter and presumably a quicker stride, which should result in a greater rate of travel (Crimes, 1970c). The V-mark angle is controlled by the angle at which the appendage is drawn across the sediment (Crimes, 1970c). Smaller V-angles result from a more posteriorly directed digging stroke, presumably resulting in a greater propulsive force relative to excavation of sediment and, thus, resulting in greater speed (Crimes, 1970c). This is supported by a correlation between small scratch mark length ratios, small V-mark angles, and shallow furrows (Crimes, 1970c). Deeper furrows are correlated with long, near transverse scratch marks indicative of slow progress and a greater force of excavation than propulsion (Crimes, 1970c).

Crimes (1970c) also claimed that greater spacing of scratch marks indicates greater stride length and thus a greater speed. This is supported by a correlation between wide spacing and short, oblique scratch marks (Crimes, 1970c). However, greater scratch mark spacing could also result from the use of a smaller number of appendages, thus, it can not be used as evidence for greater rate of movement on its own.

The presence of marginal ridges is dependent on the presence of genal spines on the trace maker and the angle at which the head is pitched (Crimes, 1970c; Seilacher, 1970). When the head is pitched down these spines are pointed up, away from the sediment. Marginal ridges are most commonly associated with shallow furrows and narrow V-marks indicating that shallow, high speed furrowing was accomplished with the head pitched up (opisthocline) while deep, slow furrowing was accomplished with the head pitched down (procline) (Crimes, 1970c; Seilacher, 1970; figure 9).

Whittington (1980) criticised the hypothesis that the postero-medial stroke of the telopodites provided both the force of digging and propulsion. This was based on a morphological analysis of the appendage structure of *Olenoides serratus*. His three arguments were that the oblique angle at which the appendages must have been drawn in would have kept the gnathobases apart, which is inconsistent with the feeding paradigm established for *Cruziana* (see below); that no modern analogue of this activity is known; and that no adequate explanation of how the simultaneous application of the digging and propulsion forces was accomplished is known (Whittington, 1980). Whittington and Almond (1987) noted that, where such data is available, the ventral cuticle of trilobites does not seem to have been mineralized and it does not seem likely that it could have sustained the stresses involved in both excavation and forward movement. Whittington (1980) went as far as to state that these objections cast doubt on trilobite production of *Cruziana* in general. This, at least, is firmly contradicted by fossil evidence.

Whittington's first argument is unacceptable since the appendage morphology of trilobites in general is poorly known (Bergström, 1973; Whittington, 1980; Seilacher, 1985); *Olenoides serratus* could well be unique in this respect. Whittington's second argument can be discounted as well since no modern analogues of trilobites are known either (Crimes, 1970c).

Whittington's third argument, based on detailed morphological analyses, may well be valid. However, there are several plausible methods by which trilobites could have circumvented this problem. The trilobite trace makers may have accomplished most of the excavating by shovelling sediment away with the cephalon (Whittington, 1980). A similar activity is shown for limulid-produced *Cruziana* by impressions of the prosoma at intervals along the furrow (Seilacher, 1985). The anterior arch of the prosoma of *Limulus* has been show to be adapted to stationary burrowing (Eldredge, 1970). Several authors (Eldredge, 1970; Bergström, 1972; Speyer, 1988) have noted that in many trilobites, the anterior border of the cephalon is vaulted like that of *Limulus* (figure 6) suggesting that it could have been used in a similar manner. Moreover, particular examples of *Rusophycus* are known where the cephalon was used to shovel out sediment (Fenton and Fenton, 1937; see *R. jenningsi*, plate 26b). Thus, it is plausible that trilobites used a shovelling action of the cephalon to assist in the production of *Cruziana*. However, independent evidence for this, such as rhythmically discontinuous marginal ridges or impressions of the cephalon, have not been noted to date in any trilobite produced *Cruziana*.

Another possibility is that the digging and propulsion actions were physically separated along the length of the trilobite's body with the digging action performed by anterior telopodites and propulsion by more posterior telopodites. Although trilobite appendages are essentially undifferentiated (Whittington, 1980), there is evidence for front-to-back gradational changes in the absolute size and relative size of both appendage branches from some *Rusophycus* (Seilacher, 1985) and from some trilobites (Whittington and Almond, 1987) suggesting subtle differences in appendage function along body length. Telopodites appear to have been larger towards the anterior end of trilobites and exites larger towards the posterior end (Seilacher, 1987). The fact that deep furrows were usually produced in a head down attitude and shallow, higher speed furrows were usually produced in a head up attitude with the anterior most appendages elevated off the sediment (Crimes, 1970c; Seilacher, 1970; figure 9) suggests that, in some trilobites at least, the anterior appendages were primarily used for digging and the posterior appendages for propulsion. The separation of digging and propulsion might also explain how trilobites could furrow with no mineralised connection between the dorsal skeleton and the appendages. If excavation at the front of the trilobite kept pace with the rate of forward movement the force of propulsion would not have to be much greater than that required for surface locomotion. This mechanism would be expected to leave more oblique scratch marks in deep burrows.

There is evidence though, that some trilobites could simultaneously apply digging and propulsion forces with the same appendage in the production of *Cruziana*. Examples of *Cruziana* ichnosp. 2 from this study show distinct, well spaced scratch marks with no evidence for two styles of appendage stroke (see *Cruziana* ichnosp. 2, plate 22a, b, c).

Another aspect of trilobite locomotion shown by their trace fossils is that they could not laterally flex their bodies to an extent sufficient for turning. *Cruziana* along curves are deeper along the inner edge of the curve and V-marks apices displaced towards the inner margin of the curve (Crimes, 1970c). Thus, it appears that trilobites turned by canting their bodies into the turn and pulling more with the appendages on the inside of the curve than the outside (Crimes, 1970c; plate 17b).

Emplacement and Preservation

The essential process for the preservation of *Cruziana* and *Rusophycus* is that they be cast by a substance which contrasts with the substrate in which the traces were emplaced (Crimes, 1975b; Baldwin, 1977a). The substrate of emplacement for successfully preserved trace fossils is usually compacted mud, since it is cohesive enough to retain the shape and ornamentation of the traces. Thus, the casting medium is usually a sand or silt. These activities may well have been carried out on other substrates, however no fossil record of this is likely. *Cruziana* and *Rusophycus* were originally thought of as open furrows and pits, emplaced at the sediment-water interface and subsequently cast by the deposition of sand (Crimes, 1975b; Seilacher, 1970). However, there are many authors who argue that fine scratch mark details emplaced in muds, would be eroded away during the deposition of sand from suspension or traction (Seilacher, 1970; Bromley and Asgaard, 1979; Goldring, 1985). There have been four different proposals to explain how fine detail can be successfully cast in sand. One suggestion is that the traces were formed intertidally (see Crimes, 1970c). Exposure during low tide could have hardened the mud substrate sufficiently to resist erosion (Crimes, 1975b). Most *Cruziana* and *Rusophycus*, however, are not associated with any independent indications of emergence (Crimes, 1975b).

Seilacher (1970) and Bromley and Asgaard (1979) suggested that *Cruziana* and *Rusophycus* could be preserved during production if the trace maker furrowed into a muddy substrate through a thin layer of sand. The surrounding sand layer would then collapse into the furrow and cover the scratch marks. Permanent preservation would occur with the deposition of a thicker sand layer, burying the trace. There are four arguments against this hypothesis. Large areas of muddy substrate covered with thin layers of sand are probably quite rare (Crimes, 1975b). Moreover, a time interval between deposition of the thin sand and the thicker sand, of sufficient duration to allow for the formation of dense assemblages of furrows and pits, would result in a lithologic discontinuity between the two sand layers (Crimes, 1975b). Such discontinuities are rarely found (Crimes, 1975b). Another problem is that a thin layer of sand could not spread out to cover many forms of *Cruziana* which can be more than 5 cm wide and less than 5 mm deep (Baldwin, 1977b). Lastly, sand is more prone to erosion than even partially compacted mud (Crimes, 1975b), thus, a thin sand layer would offer no significant protection from exposure to potentially erosive currents involved in the deposition of a thicker sand layer. It is clear, however, from the presence of peripheral sand layers in furrow infills, that at least some surface emplaced *Cruziana* and *Rusophycus* are formed in this way and infilled either by sand slumping down from the sides of the trace or by excavated sediment settling back into the trace (Seilacher, 1970; Goldring, 1985), even if these processes are not actually crucial for the preservation of the scratch mark detail.

Currently, there are two popular, opposing theories to account for the emplacement and preservation of *Cruziana* and *Rusophycus*. Crimes (1975b) and Baldwin (1977b) have supported the the view that these traces were emplaced as open surface features and were preserved by infilling with sand or silt. Goldring (1985) and Seilacher (1985) have supported the view that these traces were emplaced as true burrows along interfaces between mud and overlying sands and were infilled by collapse of the burrow after the trace maker passed along. Many of the figures given by Seilacher (1970, 1985) show *Cruziana* and *Rusophycus* being formed through a thin sand layer and impinging on a buried mud, but with the trilobite still exposed at the sediment surface. These are included as surface trails in this discussion since the trace maker would still have been influenced by the surface environment during the emplacement of the trace. This is important since the whole point of this discussion is that the difference between surface and intrastratal emplacement is important to the ethological and ecological interpretation of these trace fossils (Goldring, 1985).

Crimes (1975b) and Baldwin (1977b) presented several arguments against emplacement of *Cruziana* and *Rusophycus* as true burrows. Finely-detailed *Cruziana*, and especially *Rusophycus*, are often current oriented, indicating a strong influence of current processes on production of the traces (Crimes, 1975b; Baldwin, 1977b). Goldring (1985) stated that this could be a surface orientation to current, maintained as the trace maker made short burrows into the substrate. One would have to assume however, that the current direction at the original sediment surface during emplacement would be the same as that preserved at the interface of preservation, which is not necessarily the case. Crimes (1975b) also noted that *Cruziana* are much less common on flute scoured surfaces. This would be an unlikely coincidence in intrastratal burrows (Crimes, 1975b). Crimes (1975b) observed that solitary *Rusophycus* are often found on the base of thick sandstone beds, and that there is no good reason for a trilobite to dig straight down through a thick sand to a mud layer and then dig straight up again. Therefore these traces must have been emplaced on the surface and cast by the sand (Crimes, 1975b). Although such a behaviour is, in fact, consistent with the basic detritus feeding activity ascribed to many *Rusophycus* (see Ichnogenus *Rusophycus*) burrowing through a thick sand for a brief feed at a sand/mud interface would be prohibitively inefficient. The behaviour rejected by Crimes could, however, represent an aestivation process. It would be to the trace makers advantage to stop at a sand/mud interface as the mud would be much less oxygenated than the sand. Goldring (1985) cited examples of intersecting *Cruziana* that do that do not completely overprint each other as indicative of true burrowing, since these features must have been emplaced at different levels within the sediment and at different angles to horizontal. Surface furrows however, are not always of equal depth either along a single furrow or between different furrows. Open surface emplacement could just as easily account for this phenomenon.

The most crucial argument in support of an open surface emplacement is that the infill of most *Cruziana* and *Rusophycus* are either structureless or show cross-bedding, parallel lamination, or draped lamination with no evidence of slumping or bioturbate textures (Baldwin, 1977a). Sedimentary structures and lithology generally pass up from the trace infill into the overlying casting bed with no evident discontinuities (Baldwin, 1977a). These features indicate infilling by clean sand as fall out from suspension or under the influence of currents (Baldwin, 1977a).

Goldring (1985) however, claimed that most examples of *Cruziana* and *Rusophycus* with primary sedimentary structures in the infill are the result of intrastratal burrows having being exhumed by erosion and recast. This *ad hoc* argument is quite dubious, as it seems very unlikely that such an erosional event would not destroy the burrow itself since such a negative relief feature would create strong turbulence (Collinson and Thompson, 1982). Also, there is no reason to suppose that fine ornamentation would be any more resistant to erosion in this situation than in open furrows. Goldring (1985) claimed that thin layers of bioturbated sediment are usually found along the periphery of infills. This was interpreted (Goldring, 1985) to be indicative of incomplete erosion of the burrow infill prior to recasting. It is far more likely, however, that this thin layer represents a small amount of excavated sediment falling back into an open furrow during emplacement.

The crux of this argument is whether it is possible for fine ornamentation in open furrows to resist erosion during deposition of a sandy casting medium (Crimes, 1975b; Goldring, 1985). Crimes (1975b) carried out a detailed analysis of sediment properties as they relate to the preservation potential of fine ornamentation in exposed structures dug into muds. The final results were that the erosion of structures in consolidated and overconsolidated muds requires current velocities greater than those under which sand is deposited from traction and suspension (Crimes, 1975b). Thus, conditions which would deposit a sandy casting medium would not be capable of eroding fine detail in a consolidated muddy substrate. Moreover, the characteristics of a mud that make preservation of fine detail possible in the casting event are the same conditions necessary for the successful production and survival of the trace on the sea floor, during and immediately after emplacement (Crimes, 1975b). If a muddy substrate is sufficiently dewatered, consolidated, and cohesive to resist collapse and retain fine sculpturing during emplacement, it will resist the erosion of these same features when cast by a sand (Crimes, 1975b).

The consolidation and overconsolidation of muds can occur in three ways: burial with sufficient overburden pressure; slow accumulation under quiet water conditions; and by interbedding of sands and muds in higher energy settings where pore water in surface muds can drain into more porous underlying sands (Crimes, 1975b). Dewatered muds can also accumulate in high energy settings as fecal and pseudofecal pellets of deposit-feeders. Together, these conditions represent approximately the full range of environments in which *Cruziana* and *Rusophycus* are normally found.

Goldring (1985) did not accept Crimes' (1975b) conclusions regarding either the formation of sufficiently consolidated muds in most sedimentary setting in which *Cruziana* and *Rusophycus* are found or the actual preservation of fine detail during casting. His objections, however, were not well substantiated by thorough sedimentological analysis as was Crimes' work, and do not seem an adequate dismissal of Crimes' hypotheses.

This entire argument can be quite easily settled however, by noting that undisputed surface structures such as ***Monomorphichnus*, *Dimorphichnus***, and ***Diplichnites*** (Crimes, 1970c; Seilacher, 1985) are preserved as mud emplaced structures, cast in sand, with the same fine detail as found in ***Cruziana*** and ***Rusophycus***. Moreover, ***Cruziana*** and ***Rusophycus*** often grade into surface traces such as ***Diplichnites*** with little change in apparent depth (Crimes, 1970c; Osgood and Drennen, 1975; Seilacher, 1985) indicating that, in these cases, all three forms were produced at the surface. Thus, Crimes' (1975b) claim that fine details in mud can be preserved by casting in sand is substantiated in fact as well as in theory.

Both Crimes (1970c) and Goldring (1985) had unequivocal, specific examples of both true burrow and surface furrow forms of *Cruziana* and *Rusophycus* in specific circumstances. True burrows are identified by near circular cross-sections (plate 23a); the presence of mud stringers, clasts, and a bioturbate texture in the infill; and collapse structures in the overlying sediment (Goldring, 1985). Crimes and Baldwin, however, provided compelling arguments, for which Goldring and Seilacher had no adequate counter arguments, that support a sediment-water interface interpretation for *Cruziana* and *Rusophycus* when there is no discontinuity in lithology or sedimentary structure between the infill and overlying bed. Thus, it is the opinion of the author that, in general, *Cruziana* and *Rusophycus* should be considered to be open surface traces unless the infill or cross-sectional shape suggest otherwise. Most of the *Cruziana* and *Rusophycus* from this study are infilled with material that is identical to the overlying sandstone bed, and there is usually no indication of a burrow outline or disturbed sediment within the overlying bed. All of these specimens are, thus, assumed to have been emplaced at the sediment surface.

Ethology

The original ethological interpretation of *Cruziana* was that of simple locomotion (Crimes, 1970c). Bergström (1976) pointed out, however, that such an activity would be prohibitively inefficient in terms of the energetic cost of travel. In light of this, it is more likely that *Cruziana* represents a detritus and meiofauna feeding behaviour: grazing or browsing (Crimes, 1970c; Bergström, 1976). Detailed morphological analyses of the appendages have been particularly instructive in elucidating the mechanics of this feeding behaviour. As the telopodites are brought in towards the midline of the body, the gnathobases are rotated forward (Whittington, 1980). Thus, any food particles caught between opposing gnathobases is pushed forward as the limbs are brought inward (Whittington, 1980; Cisne, 1981; Whittington and Almond, 1987). The resulting ventro-median food groove (Cisne, 1981; figures 6, 8) is an efficient method for transporting food to the mouth since the hypostome in trilobites opens rearward, just anterior to the front-most set of limbs (Bergström, 1980; Whittington, 1980; Cisne, 1981; Whittington and Almond, 1987). Food particles, detritus and small organisms, could be transported to the gnathobases on the spines and setae at the end of the telopodites (Bergström, 1980; Cisne, 1981; Whittington and Almond, 1987). This feeding mechanism could conceivably handle live, macrofaunal prey as well since the grinding action of the gnathobases and their spines could have masticated the prey as they pushed it forward (Bergström, 1980; Whittington and Almond, 1987).

The common intergradation between *Cruziana*, *Diplichnites*, and *Rusophycus* gives an indication of the feeding strategy employed by bottom feeding trilobites. *Rusophycus* and *Cruziana* are often found joined together (Crimes, 1970c; Seilacher, 1970, 1985; plate 22a, c) and some *Cruziana* are little more than serially arranged *Rusophycus* with short segments of intervening *Cruziana* furrows (Bergström, 1976; Seilacher, 1985, figure 4). The *Rusophycus* portions of these traces have usually been interpreted as resting traces (Crimes, 1970c; Seilacher, 1985). If these were resting traces however, it would make more sense for the trace maker to just stop furrowing rather than dig a deeper pit. Since many *Rusophycus* are also considered to be feeding traces, by a mechanism similar to that for *Cruziana* (Bergström, 1973; Crimes, 1975b; Osgood and Drennen, 1975; Seilacher, 1985) it is more likely that the *Rusophycus* interspersed in *Cruziana* furrows are the result of stationary feeding to fully exploit more nutrient rich patches of sediment or process prey animals. In the same manner, *Diplichnites* segments attached to *Cruziana* furrows may result from the trace maker walking over nutrient poor zones (see *Cruziana* ichnosp. 2, plate 22a, c). *Cruziana* may be a food-searching behaviour or a deposit-feeding behaviour adapted to more diffuse detritus than *Rusophycus*. It is likely that, in many cases, these three ichnogenera were components of a more complex searching and feeding behaviour (see *Cruziana* ichnosp. 2).

While most *Cruziana* can be interpreted as feeding traces, some may still represent simple locomotion. Such furrowing would offer protection from current energy (Crimes, 1970c) or from exposure on tidal flats during low tide, as the animal moved along. In a study of the Upper Cambrian of Wales (Crimes, 1970c) *Cruziana* was much less common in low energy settings and surface traces such as *Diplichnites* were less common in high energy settings. The decrease in abundance of *Cruziana* in the low energy settings could not be attributed to preservational effects, thus its change in abundance must be a real response to changes in the hydrodynamic conditions (Crimes, 1970c). However, this may be a response to the predominance of buried, rather than surface detritus in high energy environments (Crimes, 1970). The depth of furrowing or burrowing in *Cruziana* and *Rusophycus* could as easily be a reflection of the depth of suitable food resources as of a need for protection. Differentiation between these two effects is difficult.

Environmental Associations

The large variety of potential trace makers for *Cruziana* results in a large variety of environmental associations. It is most commonly associated with the *Cruziana* ichnofacies (Crimes, 1970c; Crimes *et al.*, 1977; Kolb and Wolf, 1979; Fillion and Pickerill, 1984; Crimes and Anderson, 1985). This ichnofacies is characterised by fluctuating, moderate to low hydrodynamic energy; a variety of sediment from well sorted silts and sands to interbedded clean sands and muds; and variable sedimentation rates (Frey and Pemberton, 1984). These settings are moderately to intensely bioturbated, predominantly by horizontal burrows, surface trails, and feeding structures (Frey and Pemberton, 1984). The *Cruziana* ichnofacies is commonly found in estuaries, bays, lagoons, tidal flats, continental shelves and epeiric seas (Frey and Pemberton, 1984). These settings have an abundant supply of detritus and are quiet enough for this to settle out, providing a food supply for the detritus-feeding types of *Cruziana* behaviour and supporting a large enough population of other infauna for predatory forms of the *Cruziana* behaviour.

Cruziana is most common in thinly interbedded sands and muds (Baldwin, 1977a; Crimes *et al.*, 1977; Fritz and Crimes, 1985). Lithologic discontinuities and, thus, finite gaps in sedimentation are necessary for the production and preservation of these traces as recognisable trace fossils (Crimes, 1975b; Baldwin, 1977a). The most likely settings for this to occur range from moderate energy shelf seas to intertidal flats. These environments experience alternating deposition of sand and mud as well as periods of non deposition. As well, they provide a number of mechanisms for producing cohesive muds: exhuming relict muds; accumulation of mud pellets created by deposit feeders; and interbedding of sand and mud that causes dewatering of surface muds (Crimes, 1975b). Incipient *Cruziana* may well be produced in other settings but the likelihood of their being preserved as recognisable trace fossils is much less.

Although *Cruziana*, and other scratch marked traces of this type, are associated with at least partially consolidated muds, they should not be used to imply the presence of a true *Glossifungites* ichnofacies (*sensu* Ekdale *et al.*, 1984). These traces are extremely widespread in the Paleozoic and often occur in the presence of intense intrastratal deposit-feeding bioturbation (see Chapter 3) which is inconsistent with the concept of the *Glossifungites* ichnofacies (Frey and Pemberton, 1984). Well preserved *Cruziana* and *Rusophycus* are probably associated with substrate consistencies marginal to that of a true *Glossifungites* ichnofacies. These traces might be generated in non cohesive, or poorly cohesive muds but the scratch mark pattern and precise furrow form would not be preserved (Crimes, 1975b), and any resulting trace fossils would not be recognisable.

Cruziana is very rare in monolithic shales (Baldwin, 1977a). The quiet water settings responsible for these deposits do not produce cohesive enough muds for the construction of these traces (Crimes, 1975b), nor do they have the lithologic discontinuities necessary for their preservation. Moreover, such environments are often either quiet water dysoxic or anoxic basins, unsuitable for most epifauna, or deep water settings far from shore, where the rate of fallout of detrital organics is too slow and the detritus too refactory (Nybakken, 1982) to support unorganised surface deposit-feeding (Seilacher, 1974).

Cruziana is also rare in monolithic sandstones and sandstone-dominated settings (Baldwin, 1977a) although this is to be expected as there are few lithologic discontinuities for preservation of these traces. *Cruziana* may have been produced in these high energy settings as simple locomotion traces and for protection from strong currents (Crimes, 1970c), but these would have little or no preservation potential when formed in loose sand.

Crimes *et al.* (1977) noted a positive correlation between the size of *Cruziana* and *Rusophycus* and the thickness of the sandstone beds under which they are preserved. They investigated three explanations for this: intrastratal formation, in which only larger trilobites could have burrowed through thicker beds; a correlation between thicker beds and more erosive currents, which would remove smaller traces; or an environmental preference. The first explanation can be discounted if most of these trace fossils were emplaced as surface traces (Crimes *et al.*, 1977). The second explanation is discounted since many thick beds with *Cruziana* and *Rusophycus* preserve fine surface traces such as *Monomorphichnus* (Crimes *et al.*, 1977). The third explanation is the most plausible (Crimes *et al.*, 1977). Small trilobites would be in danger of being swept away in high energy environments and thus, inhabit quiet water environments which produce thinly bedded deposits (Crimes *et al.*, 1977). There are three possible explanations as to why larger *Cruziana* are not found in thinly bedded deposits. Thin casting sands might not completely infill these traces and, when left as negative relief features on the sea floor they would generate bottom turbulence and be destroyed. Another possibility is that quiet water, thinly interbedded silt and mud settings may not receive a supply of large enough detritus particles for large trilobites to handle. The third possibility is that larger trilobites relied less on detritus-feeding and more on predation (see Ichnogenus *Rusophycus*, Ethology), possibly specialising on stationary infauna such as filter-feeders. This would explain observations of large *Cruziana* and *Rusophycus* in sandstone dominated deposits along with abundant shafts (Baldwin, 1977a; Ichnogenus Rusophycus, Ethology; Chapter 3, Unit 3).

The most common paleoenvironments with which *Cruziana* have been associated are: mixed, mud, and sand intertidal flats (Baldwin, 1975; Kolb and Wolf, 1979; Legg, 1985; Crimes *et al.*, 1977; Baldwin, 1977a); shallow subtidal settings (Baldwin, 1977a); and stable shelf seas (Baldwin, 1975; Bergstrom, 1976). Small forms (*Cruziana stromnessa* and *C. problematica* (=*Isopodichnus*) and *Rusophycus eutendorfensis* (=*R. didymus*)), are often found in fresh water deposits (Hakes, 1972; Bromley and Asgaard, 1979; Hakes, 1985) and shallow to emergent marginal marine settings (Hakes, 1985; Demathieu, 1985). Some authors go so far as to regard "*Isopodichnus*" as a fresh water indicator in the Mesozoic and late Paleozoic (Trewin, 1976; Hakes, 1985) although many marine examples are known (Bromley and Asgaard, 1979). Rare occurrences of *Cruziana* and *Rusophycus* are also known from marginally dysoxic deposits (Jordan, 1985); tidal channels (Legg, 1985); and lagoons (Baldwin, 1975). Many of these environments were not commonly frequented by trilobites (B.D.E. Chatterton, pers. comm., 1988).

Ichnotaxonomy

The history of the name "*Cruziana*" was discussed in detail by Osgood (1970, p. 303). These trace fossils were originally named *Bilobites* d'Orbigny 1839, however this term had already been applied to an unrecognised genus of trilobite, and the sedimentary structures were renamed *Cruziana* by d'Orbigny in 1842 (Osgood, 1970).

Cruziana is one of a number of similar ichnogenera produced by arthropods: *Diplichnites* and *Rusophycus*, and non arthropods: *Scolicia*. *Diplichnites*, a surface walking trace, is differentiated by its lack of distinct lobes and the presence of a distinct median gap (Crimes, 1970c; Osgood, 1970; Bergström, 1973; Häntzschel, 1975). *Rusophycus*, a stationary digging trace, is differentiated by its oval shape compared to the long furrow of *Cruziana* (Crimes, 1970c, 1975a; Häntzschel, 1975). *Scolicia* consists of forms similar to both *Cruziana* and *Rusophycus* (Smith and Crimes, 1983) but has fine brush marks and smooth, transverse to oblique ridges rather than scratch marks. *Scolicia* is interpreted as the result of heart urchins and, in some cases, gastropods performing similar activities to those which produce *Cruziana* and *Rusophycus*, but with different mechanics of production (Smith and Crimes, 1983).

Crossochorda Schimper 1879 was applied to forms intermediate between *Cruziana* and *Rusophycus* (Osgood, 1970). However, such is the continuity of intermediate forms that this ichnogenus does not actually simplify the situation at all (Osgood, 1970). Thus, Osgood (1970) advocated combining *Crossochorda* under *Cruziana*, since all forms of *Crossochorda* must involve some degree of forward movement. *Crossopodia*, M'Coy, 1851 is a trace of similar morphology, inferred mechanics of formation, and ethology to *Cruziana* (Bergström, 1973; Häntzschel, 1975). As such, it should probably be made a junior synonym of *Cruziana*. *Isopodichnus* Bornemann 1889 is identical to *Cruziana* in all aspects except is small size (Seilacher, 1970; Bromley and Asgaard, 1979). The ichnotaxonomic problems associated with this ichnogenus are discussed below. *Rouaultia* de Tromelin 1878 is a trace similar to *Cruziana* but without scratch marks. It was synonymised with *Didymaulichnus* by Young (1972) and interpreted to be the crawling or ploughing trace of a soft bodied animal. However, poorly preserved *Cruziana*, without scratch marks, can be mistaken for *Rouaultia* (see Crimes, 1970c) and specimens must be compared with any *Cruziana* in the same strata to see if they share any specific morphological features that would suggest that they are, in fact poorly preserved *Cruziana*. *Didymaulichnus* and *Didymaulyponomos* are similar to *Cruziana* but are smooth or faintly ridged (Young, 1972; Bradshaw, 1981). They are produced by ploughing rather than by digging as in *Cruziana*.

Distinguishing *Cruziana* from *Diplichnites* and *Rusophycus* can be difficult as all three forms can intergrade with each other (Crimes, 1970c; Osgood and Drennen, 1975; Seilacher, 1985) and there are many examples intermediate between *Cruziana* and *Diplichnites* (Crimes, 1970c). Intergradation of different ichnogenera and ichnospecies poses certain taxonomic problems. The strategy adopted by most authors in these cases has been to give the entire structure the name of the dominant element (Bergström, 1976; see also Pemberton and Frey, 1982). It is the opinion of the author, however, that each component should be named separately and the interrelationship described. For example, in short stretches of *Cruziana* separated by *Rusophycus*, each component should receive separate ichnotaxonomic treatment (see Chapter 4, Ichnotaxonomy).

The ichnotaxonomy of trilobite and other arthropod produced trace fossils suffers from a conflict between two opposing philosophies (Osgood, 1970). In most cases, especially at the ichnogeneric level, ichnotaxonomy is set up to reflect the behaviour rather than the identity of the trace maker (Chamberlain, 1971; Fürsich, 1974b; Pemberton and Frey, 1982; Fillion and Pickerill, 1984; Gureyev, 1985; see Chapter 4). There are instances, however, where trace fossils preserve features thought to represent taxonomically significant anatomical features of the trace makers (Crimes, 1970c; Seilacher, 1970; Gureyev, 1985; Pemberton *et al.*, 1988). These features are often incorporated into the taxonomy of the trace fossils, either because this makes them useful as index fossils or because they are the only distinct morphological features available (see Seilacher, 1970; Pemberton *et al.*, 1988). This conflict is most clearly expressed in the taxonomy of *Cruziana* and *Rusophycus*. These two ichnogenera preserve several features which reflect detailed anatomical features of the trace makers including appendicular claw and spine patterns; the general outline of the trace maker (*Rusophycus*); and the presence of genal and pleural spines.

This conflict is seen in two aspects of the ichnogeneric classification of arthropod traces. Seilacher (1970, 1985) appeared to advocate restricting *Cruziana* (=*Rusophycus*) to only those traces produced by trilobites (see also Hakes, 1985). However, many authors are of the opinion that ichnosystematics, at the ichnogeneric level at least, should not be influenced by the identity of the trace maker, especially in situations like this, where there are no differences in general morphology or ethology between the forms in question (Bromley and Asgaard, 1979; Fillion and Pickerill, 1984; Gureyev, 1985). There is also the problem that in practice, although there are some *Cruziana* and *Rusophycus* that are obviously of non-trilobite origin (Seilacher, 1985), the number of transitional forms between traces of obvious trilobite and non-trilobite origin makes the ichnotaxonomic separation of non-trilobite produced traces impractical (Seilacher, 1985). Seilacher (1985) hoped that this segregation would become possible in the future. If such a system is adopted, however, it would, as the present number of transitional forms suggests, become so misleading and complex that only a few experts would be qualified to make ichnotaxonomic assignments. Therefore, it is the opinion of the author that such a system should not be employed.

Isopodichnus is the only non trilobite produced trace fossil with forms similar to *Cruziana* and *Rusophycus* that has been placed in a separate ichnogenus (Seilacher, 1970; Hakes, 1985). *Isopodichnus* consists of small forms, less than 10 mm wide (Trewin, 1976; Bromley and Asgaard, 1979). It is thought to be produced by branchiopods and is used as a brackish to non-marine indicator (Seilacher, 1970; Hakes, 1985). It is because of this usefulness as an environmental indicator that many authors maintain it as a separate ichnogenus (Seilacher, 1970; Hakes, 1985). As there are no morphological differences except for size however, some authors have chosen to place it in synonymy with *Cruziana* and *Rusophycus* (see *C. problematica*, *C. stromnessa*, *R. eutendorfensis*) reasoning that environmental affiliation should not be a criterion for ichnotaxonomic assignment (Bromley and Asgaard, 1979; Fillion and Pickerill, 1984). In practice, smooth intergradations in size, with consistent width to length ratios, have been observed within samples of *Isopodichnus* and *Rusophycus*, indicating that both forms were made by different ontogenetic stages of the same species of trilobite (Radwanski and Roneiwicz, 1963; Crimes, 1970c). Moreover, many specimens of "*Isopodichnus*" are found in marine deposits (Crimes, 1970c; Fillion and Pickerill, 1984). Thus, there are no consistent reasons, with respect to either environmental associations or trace maker identity, for separating this ichnogenus from *Cruziana* and *Rusophycus*. Thus the author follows Bromley and Asgaard's (1979) practice of uniting *Isopodichnus* with *Cruziana* and *Rusophycus*.

Another point at which the two philosophies conflict is the relationship between *Cruziana* and *Rusophycus*. Seilacher (1970) pointed out that as these two ichnogenera are formed by the same mechanisms, and *Cruziana/Rusophycus* pairs with identical scratch mark patterns and identical trace makers, can be identified. As the only difference between them is ethological, Seilacher (1970) was of the opinion that there is no justification for separating the two ichnogenera. According to Seilacher (1985) this practice of combining *Rusophycus* under *Cruziana* has been generally accepted. In fact, however, most authors have continued to separate these ichnogenera (Bergström, 1973, 1976; Crimes, 1975a, 1975b, 1987; Baldwin, 1977a; Crimes, *et al.*, 1977; Bradshaw, 1981; Pickerill, *et al.*, 1984; Crimes and Anderson, 1985; Legg, 1985). The reason for this is that, while combining the two ichnogenera might simplify their biostratigraphic use in a small way, it ignores the fundamental and easily identifiable differences in morphology, ethology, and ecology between the two forms (Osgood, 1970; Crimes, 1975a, 1975b).

The conflict between ethology and trace maker taxonomy is most evident at the ichnospecific level of trilobite ichnotaxonomy. According to Seilacher (1970, 1987), *Cruziana* (=*Rusophycus*) ichnospecies are easily distinguished on the basis of shape and surface ornamentation, and correspond to certain, although usually unrecognised, trilobite taxa and thus, should be as useful as index fossils. Variations due to ecology, behaviour patterns, anatomical features not diagnostic of the trace maker, and preservation should be regarded as intraspecific variation (Seilacher, 1970; Kolb and Wolf, 1979). Some of these variations however, can be shown empirically to be of stratigraphic significance and have, therefore, been incorporated into the ichnotaxonomy (Seilacher, 1970). This system of ichnotaxonomy has been accepted by most authors (see Osgood, 1970; Osgood and Drennen, 1975) and many *Cruziana* ichnospecies, thus defined, have been used as index fossils, especially in the upper Cambrian and Ordovician (see Seilacher, 1970, Crimes, 1975a, 1975c; Baldwin, 1977a; Crimes *et al.*, 1977; and Chapter 4, Applied Ichno-chronostratigraphy).

The underlying assumption in Seilacher's view of trilobite ichnotaxonomy is that scratch mark patterns reflect the appendicular claw patterns and thus the identity of the trilobite trace makers (Crimes, 1970c; Seilacher, 1970; Crimes *et al.*, 1977; Legg, 1985). There are several problems with this assumption, however. A certain claw pattern can produce different scratch mark patterns depending on the angle of contact between the sediment and appendage; the angle of movement with respect to the appendage axis; the force or depth of impression (Seilacher, 1962, figure 2; Osgood, 1970; Osgood and Drennen, 1975; Crimes *et al.*, 1977); and the sediment consistency (Crimes, 1975b). Thus there is no easily determined relationship between scratch mark pattern and claw pattern; it must be carefully determined in every case. Moreover, there are no concrete relationships established between claw patterns and trilobite taxonomy at any taxonomic rank, and especially at the generic and specific ranks (G. Edgecombe, pers. comm., 1987) since the appendage morphology of trilobites in general is very poorly known (Whittington, 1980; Seilacher, 1985). Thus, scratch mark patterns can not be used, at present, to define trilobite taxa, whether real or hypothetical, of any particular rank from subspecies to genus and probably up to at least order.

In fact, the actual identification of the trace makers of particular *Cruziana* and *Rusophycus* is a complex, rarely successful process which must be repeated at every occurrence, even for the same ichnospecies (Bergström, 1973). It involves a detailed, statistical analysis of the morphology and ornamentation of the traces and a similar analysis of the body fossil data for the same deposits (Bergström, 1973; see Bergström, 1973 and Crimes, 1975b for examples). Contrary to Crimes (1975b), the same ichnospecies in another occurrence can not be used to assume the same taxon of trace maker at different geographic or stratigraphic locations (Bergström, 1973).

Seilacher's ichnotaxonomic system suffers from several problems in practice as well. Some trilobite ichnotaxa have long geologic time ranges with little change in morphology. *Rusophycus rugosa*, for example, ranges from the Lower Cambrian in North America (this study) to the middle Ordovician of Europe (Crimes *et al.*, 1977), with no change in scratch mark pattern (T.P. Crimes, pers. comm., 1987). Given the time and geographic separation of these two occurrences, it is unlikely that the trace makers for each are very closely related (see Chapter 4). Thus, a given ichnospecies can be produced by more than one taxon of trilobite. This should be expected since morphology of the anatomical features responsible for the production of trace fossils will be, by nature, highly functional and should be expected to display a high degree of convergence both in the behaviour they represent (Gureyev, 1985) and in the relevant body parts (see Osgood, 1970; Pemberton and Frey, 1982).

Another problem which casts doubt on Seilacher's (1970) assumptions concerning the one-to-one relationship between trilobite taxa and *Cruziana* ichnospecies is the intergradation of different ichnospecies of *Cruziana* in single specimens. This is common in groups of similar ichnospecies such as *C. furcifera*, *C. goldfussi*, and *C. rugosa* (Kolb and Wolf, 1979). It also occurs between markedly dissimilar ichnospecies as in a sample of *Cruziana* and *Rusophycus*, from this study, which grades from *Cruziana semiplicata* to *Rusophycus bilobatum* and on into *Cruziana* ichnosp. 4 (plate 24a). Thus, an individual taxon of trilobite is capable of producing a much broader range of *Cruziana* ichnospecies than would be apparent from Seilacher's (1970) paper, simply by engaging in different patterns of behaviour.

The dubious nature of Seilacher's (1970) one-to-one relationship between trilobite taxa and ichnospecies of *Cruziana* should be obvious when one considers that there are thousands of genera of trilobites known in the literature (G.D. Edgecombe, pers. comm., 1988), a fair proportion of which must have crawled and furrowed on the bottom, and only about 50 known ichnospecies of *Cruziana* and *Rusophycus* resulting from these activities (figures 24, 25).

Thus, the present system of *Cruziana* and *Rusophycus* ichnotaxonomy, constructed for biostratigraphic utility, is seriously flawed since the the relationship between ichnospecies of *Cruziana* and *Rusophycus*, and certain trilobite taxa is far more complex than Seilacher (1970) presumed. This system should be abandoned in favour of a system based on ethology, since the traces preserve a great deal of information concerning the behaviour of the trace makers which can not be obtained elsewhere (Crimes, 1970c). In spite of this, all the ichnospecies of *Cruziana* and *Rusophycus* in this study have been assigned to recognised ichnospecies, using currently recognised criteria of shape and scratch mark pattern, since a detailed taxonomic revision of these ichnogenera was not attempted in this study.

Cruziana arizonensis Seilacher, 1970
plate 24d

Diagnosis

Cruziana consisting of medial lobes separated by a narrow median groove and bordered by lateral lobes. There are no marginal ridges. Medial lobes have coarse, double or triple, oblique scratch marks, lateral lobes are covered with fine, longitudinal brush marks. (after Seilacher, 1970)

Stratigraphic Range

Cruziana arizonensis is known from Middle Cambrian deposits (Seilacher, 1970).

Occurrence

One specimen of *Cruziana arizonensis* was found on float in unit 5. The most likely source for this specimen was unit 6. The sandstone and shale lithology of the sample was unlike that of the overlying Mount Whyte or Cathedral formations.

Description

The specimen consists of a 90 mm long, 45 mm wide fragment with rounded, high relief lateral lobes and narrow, low relief medial lobes separated by a distinct, median groove. There is no evidence of marginal ridges. The medial lobes are 3-5 mm wide and 3-5 mm in relief. The lateral lobes are 10-20 mm wide and 4-11 mm in relief. The relief and width of the lobes varies along length.

The medial lobe scratch marks are coarse, straight, 60^{0} to near transverse, and equally paired. The lateral lateral lobes are covered by indistinct, fine, longitudinal brush marks. The medial lobe scratch marks are cross-cut by the lateral lobes.

Discussion

Seilacher's (1970, figure 7-9) drawing of *Cruziana arizonensis* shows that it consists of narrow, flat, low relief medial lobes bordered by high relief, well rounded lateral lobes. The lateral lobes cross-cut the outer edge of the coarse, near transverse medial lobe scratch marks (Seilacher, 1970). The lateral lobes are covered by very fine, longitudinal brush marks. The trace maker of *Cruziana arizonensis* must have utilised both the exite and telopodite branches in the production of this trace, with the exites producing the lateral lobes. The difference in scratch mark morphology and the sharp discontinuity between the two lobes negates the possibility that one appendage branch produced both lobes.

The fact that the lateral lobes cross-cut the outer ends of the medial lobe scratch marks suggests that the medial lobes were made by appendages anterior to those that produced the lateral lobes. A similar front to back differentiation in appendage function has been proposed for the formation of *Cruziana barriosi* (Baldwin, 1977a). The shallow, flat medial scratch marks suggest that the telopodites that produced them were primarily responsible for propulsion. *Cruziana arizonensis* probably represents a surface deposit-feeding activity in which detritus and small infauna are caught up on the exites as they are dragged through the sediment. This food material could either be continuously scraped off by the rear telopodites and transferred to the ventro-median food groove or the trace maker could have stopped periodically to perform this action.

The only diagnostic morphological difference between *Cruziana arizonensis* and *C. semiplicata* is the absence of marginal ridges in the former (Seilacher, 1970). However, as Seilacher (1970) pointed out, neither marginal grooves nor lateral lobes are present in all specimens of *C. semiplicata*, even though they are diagnostic features (Seilacher, 1970). Thus there is no consistent morphological or behavioural basis for separating these two ichnospecies. Moreover, the presence of genal spine ridges is not a good criterion for separating ichnospecies since it can vary both with the anatomy of the trace maker and the angle at which the cephalon is held. This makes it impossible to resolve the significance of the presence of marginal ridges in a sample without a detailed examination of all specimens (Bergström, 1976). The mode of function of the appendages should be given priority in ichnotaxonomy over features such as marginal ridges (Bergström, 1976). The single specimen in this study conforms to Seilacher's (1970) diagnosis and is almost identical to his line drawing (Seilacher, 1970, figure 7-9). For this reason it was separated from the other specimens with lateral lobes, *C. semiplicata*, in this study as the latter had little difference in relief between the medial and lateral lobes.

The only practical basis for separating *Cruziana arizonensis* and *C. semiplicata* is a difference in stratigraphic and geographic distribution: *C. arizonensis* being found mainly in the Middle Cambrian of North America; and *C. semiplicata* being found mainly in the Upper Cambrian of Europe (Seilacher, 1970). This separation is based on an assumed difference in trace maker rather than any demonstrable difference in morphology. Thus, *C. arizonensis* should be synonymised with *C. semiplicata*.

Cruziana clavata Hall, 1852
plate 23b, d, e

Diagnosis

Cruziana consisting of narrow, straight sided furrows with vertical, bulging sides; flat to slightly lobed tops; and width to height ratios of approximately 2:1. Width and height are constant along length. Scratch marks are are not diagnostic. (after Osgood and Drennen, 1975).

Stratigraphic Range

Cruziana clavata is known from Silurian deposits (Osgood and Drennen, 1975).

Occurrence

Cruziana clavata was found in subunits 4r, 4t, and 6c and on float at Lake Louise (Lake Agnes).

Description

Specimens consist of high relief, weakly bilobed furrows. Furrow width averages 20 mm. The sides are 5–10 mm high and vertical to bulging, pinching back in at the base by up to 3 mm. The Lake Louise traces run straight over the exposed lengths, up to 200 mm. The Redoubt Mountain traces are less than 50 mm long and often have blunt, faintly bilobed, undercutting terminations at one end. One of these specimens inscribes a broad arc with tangential ridges running along the inner lobe of the turn (plate 23e). All specimens had vague, oblique scratch marks.

Discussion

This ichnospecies is distinguished by its U-shaped cross-section; its consistent dimensions along length; and the sharp transition from steep sides to a flat, weakly lobed top (Osgood and Drennen, 1975). Scratch marks are never well preserved and are not used as ichnotaxonomic features (Osgood and Drennen, 1975). The ends of the furrows slope smoothly down to the surrounding bedding surface, narrowing only slightly (Osgood and Drennen, 1975, plate 3 figure 3). The slightly undercut sides and blunt, bulbous terminations on some of the specimens from this study suggest that this trace was either a very deep furrow or a true burrow. The tangential ridges across the top of curved portions of one of the furrows suggest that the trace maker turned in a series of steps rather than a smooth motion.

Cruziana clavata is similar to *C. pormensis*, but lacks the deep median groove, well rounded lobes, and distinct scratch marks along the lobes and sides of the trace fossil. The latter difference may be a result of differences in the consistency of the substrate, however, the former suggest a different excavation style. Both ichnotaxa have cross-sectional shapes suggestive of true burrows or deep furrows. Both ichnotaxa have the scratch marks that are too fine to account for the depth of the structures. This suggests that the traces were traversed repeatedly after production. Some specimens of *Cruziana* ichnosp. 2 have the same overall shape as *C. clavata*. However, the scratch marks of *C.* ichnosp. 2 are distinct, well separated, and deeply impressed. This is not consistent with repeated use.

Cruziana furcifera d'Orbigny, 1842

plate 21c

Diagnosis

Cruziana consisting of wide, gently rounded lobes separated by a narrow median groove. The lobes are covered with fine, regular, parallel scratch marks that swing from oblique to near longitudinal at the median groove. There are no lateral lobes or marginal ridges. (after Seilacher, 1970; Crimes and Marcos, 1976; Pickerill *et al.*, 1984)

Stratigraphic Range

Cruziana furcifera is known to range from middle Tremadoc to Llandeilo deposits (Crimes, 1970b).

Occurrence

A single specimen of *Cruziana furcifera* was found on float at Lake O'Hara.

Description

The specimen consists of a 90 mm long, 70 mm wide, bilobed furrow without lateral lobes or marginal ridges. It is fragmented at one end while the other consists of a round, gently sloping termination. The lobes are low and slightly rounded with an indistinct median groove. Scratch marks are mutually parallel, fine, and paired. The distance between pair elements varies periodically, imparting a wavy appearance. They are oblique at the outer margins of the trace and curve back to near longitudinal in the median groove.

Discussion

Cruziana furcifera consists of wide, flat lobes with a dense covering of long, fine scratch marks that curve from oblique to near longitudinal near the median groove. Individual scratch marks are made up of fine, anastomosing scratches. Scratch marks are organised into wide sets of mutually parallel marks (Bergström, 1976), and must have been produced by a comb-like appendage, most probably the exite branch (Bergström, 1973, 1976; Crimes, 1975a). Although the scratch marks are oblique to the furrow trend near the outer margins, the length of the scratch marks are indicative of passive dragging rather than active digging (Bergström, 1973, 1976; Crimes, 1975a) at least along the median portion of the scratch mark. *Cruziana furcifera*, and *C. goldfussi*, probably result from a surface deposit-feeding behaviour in which detritus is scraped off the sediment surface by the exites. Propulsion was probably effected by more anterior appendages (Bergström, 1973, 1976; Crimes, 1975a). Evidence of this activity would be overprinted by the dragging of the exites (Bergström, 1976; Crimes, 1975a). Bergström (1973) suggested that some digging may have been accomplished by the cephalon although this would be counter-productive in a surface deposit-feeding trace. The oblique, curving orientation of the scratch marks indicates that the exites were drawn in and lifted back out as they were dragged along, possibly related to a mechanism to scrape food off the exite fringe or to push detritus medially towards the gnathobases. The dense pattern of scratch marks indicates that a large number of appendages were dragged along. *Cruziana furcifera* and *C. goldfussi* are usually interpreted to be shallow surface traces (Pickerill *et al.*, 1984). However, some steep-sided forms are known from both ichnospecies (Pickerill *et al.*, 1984). These forms are as deep as they are wide, thus it is more likely that they were burrows rather than furrows (Pickerill *et al.*, 1984).

Cruziana furcifera and *Cruziana goldfussi* are differentiated by the presence of marginal ridges in *C. goldfussi* (Seilacher, 1970). However, marginal ridges have been found intermittently within specimens of *C. furcifera* (Pickerill *et al.*, 1984) thus their presence does not seem to be a reliable diagnostic feature (Bergström, 1976). There are, however, two distinct groups within these two ichnospecies based on scratch mark patterns (see Seilacher and Crimes, 1969; Crimes, 1970b; Crimes and Marcos, 1976; Baldwin, 1977a). The first is a dense pattern of oblique to medially longitudinal scratch marks, each made up of two or more delicately anastomosing elements and is typical of most *Cruziana* *furcifera*. The second consists of distinct, single, regularly spaced, parallel, comb-like scratch marks, near longitudinal over the width of the lobes. This scratch marks morphology is typical of most *Cruziana goldfussi*. This separation by scratch mark pattern is also seen in the respective type specimens (D. Fillion, pers. comm., 1987). Thus, *Cruziana furcifera* and *C. goldfussi* should be rediagnosed so that they correspond to the first and second scratch mark patterns respectively.

Cruziana goldfussi Rouault, 1850
plate 21e

Diagnosis

Cruziana consisting of wide, gently rounded lobes separated by a narrow median groove. The lobes are covered with fine, regular, parallel scratch marks that swing from oblique to near longitudinal at the median groove. Marginal ridges are present on one or both sides of the trace. There are no lateral lobes. (after Seilacher, 1970; Crimes and Marcos, 1976; Pickerill *et al.*, 1984)

Stratigraphic Range

Cruziana goldfussi is common from deposits of Arenig to Llandeilo age, although it may range down into Tremadocian strata (Crimes, 1970b; Crimes, 1975a)

Occurrence

Cruziana goldfussi was found in subunits 2j and 2q, and on float at Lake O'Hara.

Description

The Lake O'Hara specimen consists of a low relief wide furrow, fragmented at either end, with smooth, irregular swellings in width and relief, which vary from 40–55 mm and 5–10 mm respectively. The broad medial lobes are separated by a deep median groove. Scratch marks are very long and run approximately 20° to the trend of the trace, curving toward longitudinal near the median groove. They are closely and very regularly spaced at about 1 mm apart. The scratch marks are organised into wide, cross-cutting sets but the number of scratch marks per set could not be ascertained. The furrow grades into a *Cruziana rugosa* at a large swelling at one end of the furrow. The Redoubt Mountain specimens were not recovered as intact furrows, but as fragments of the characteristic scratch mark pattern.

Discussion

Cruziana goldfussi is similar in morphology, inferred ethology, and mechanics of formation to *Cruziana furcifera*. It differs from *C. furcifera* in the comb-like regularity of the scratch marks and their straight, near longitudinal orientation. The regularity of the scratch marks suggests that only one set appendages was dragged. The length and straightness of the scratch marks indicates that the causative appendages were held more or less stationary as they were dragged along. *Cruziana furcifera*, *C. goldfussi*, and *C. rugosa* often grade into each other in the same furrow. Thus, they must represent different behavioural patterns of the same trace maker.

The taxonomic assignment of these specimens was made on the basis of scratch marks (see *Cruziana furcifera*) rather than on the presence of marginal ridges. None of the specimens in the present study had marginal ridges.

Cruziana plicata Crimes *et al.*, 1977

plate 23f

Diagnosis

Cruziana consisting of two, flat to slightly rounded lobes with distinct, paired or single, straight to slightly curved scratch marks, oriented roughly 45^{o} to the trend of the trace fossil (after Crimes *et al.*, 1977).

Stratigraphic Range

Cruziana plicata is known from Lower Cambrian deposits (Crimes *et al.*, 1977), along with a possible Devonian occurrence (Bradshaw, 1981).

Occurrence

Specimens of *Cruziana plicata* were found in unit 2, unit 4, and on float in unit 6. The ultimate source for the float specimen was undoubtedly unit 6. There was also a single occurrence on float at Lake O'Hara.

Description

All specimens consist of furrows that were fragmented at both ends, with lengths that range up to 250 mm. They consist of a set of 1 mm relief, flat topped lobes separated by a shallow median gap or groove. Total width averages 18 mm. Scratch marks extend across the full width of the lobes. They are coarse, straight to slightly curved medially, paired or single, and closely and irregularly spaced.

Discussion

Cruziana plicata consists of wide, flat to slightly rounded lobes, without lateral lobes or marginal ridges (Crimes *et al.*, 1977). This ichnospecies is very similar to *Cruziana semiplicata*, the only differences being the consistent lack of lateral lobes and marginal ridges within populations and the presence of paired rather than triple scratch marks (Crimes *et al.*, 1977). None of the above features are consistent in *C. semiplicata* however (Seilacher, 1970; Crimes 1970c; Crimes *et al.*, 1977), as it is defined by Seilacher (1970). Thus, while *C. plicata* may indeed be a distinct class of *Cruziana*, the current diagnosis of *C. semiplicata* subsumes that of *C. plicata*. The only present justification for the separation of these two ichnospecies is the apparent stratigraphic separation of populations consistently lacking some of the characteristic *C. semiplicata* features. From the standpoint of ethology and morphology, the two ichnospecies should be revised so that all forms of *Cruziana semiplicata* without lateral lobes are placed in *Cruziana plicata*.

The consistent lack of lateral lobes in populations of these traces suggests that either the trace makers were incapable of bringing the exites into contact with the sediment or the exites were only lightly brushed against the sediment and evidence for this has been removed. The specimens of *Cruziana plicata* in this study were consistently smaller than specimens of *Cruziana semiplicata*. None of the specimens of *C. plicata* have any indication of lateral lobes or marginal ridges. Thus, they probably represent a different species of trace maker, one which did not use its exite branches to scrape the sediment.

Cruziana pormensis Crimes *et al.*, 1977

plate 23a, c

Diagnosis

Cruziana consisting of high relief, vertical sided, well rounded lobes separated by a narrow median groove. The sides form narrow lateral lobes with horizontal ridges running parallel to the trace. The inner lobes have fine, oblique scratch marks that curve back medially. (after Crimes *et al.*, 1977)

Stratigraphic Range

Cruziana pormensis is known from the Lower Cambrian of Spain (Crimes *et al.*, 1977).

Occurrence

A single specimen of *Cruziana pormensis* was found in subunit 4x.

Description

The specimen consists of a 36 mm deep, predominantly cylindrical tunnel bounded by shale on the bottom and sides. The lower surface consists of two well rounded lobes separated by a 2–3 mm deep median groove. The scratch marks are moderately coarse, 35–50° from longitudinal at the outer lobe margins and curve smoothly to near longitudinal in the median groove. The sides are covered by vague, horizontal to slightly vertically inclined ridges, 1 mm wide and up to 30 mm long. There is no evidence of structure within the quartzite infill.

Discussion

Cruziana pormensis consists of deep, steep-sided furrows with well rounded lobes separated by a deep median groove (Crimes *et al*., 1977). The sides of the of the furrow and the margins of the lobes consist of horizontal to inclined, fine, smooth longitudinal ridges and scratch marks (Crimes *et al*., 1977). Crimes *et al*. (1977) differentiated this ichnospecies from *C. semiplicata* by the presence of marginal ridges in the latter. However, marginal ridges are not a consistent feature of *Cruziana semiplicata* as defined by Seilacher (1970). From an examination of Crimes *et al*.'s (1977) plates, it seems that the two distinctive features of *Cruziana pormensis* are the extreme depth of the trace fossil compared to the flat, low relief lobes of *Cruziana semiplicata* (see Crimes, 1970c; Seilacher, 1970) and the fact that the "lateral lobes" in *C. pormensis* are little more than a zone of smooth, longitudinal scratch marks along the side of the furrow. These lateral scratch mark zones appear to have been made by the telopodites or pleurae dragging against the sides of the furrow (Crimes *et al*., 1977). Thus, they are not analogous to the lateral lobes of *Cruziana semiplicata*.

The specimen from this study matches the description and figures of the specimen of *Cruziana pormensis* in Crimes *et al*. (1977) from the Lower Cambrian of Spain except that the lateral scratch marks are coarser and smoother than those in Crimes *et al*. (1977). This probably reflects a different trace maker with stubbier pleurae. As well, the specimen from Spain is much shallower and does not have the circular cross-section of this specimen. As it is the only other specimen known, it is impossible to evaluate the ichnotaxonomic significance in this difference of cross-sectional shape.

The circular cross-section and clean quartzite infill, surrounded by shale, indicates that the specimen from this study was an open burrow. The trace was either a permanent or semipermanent shelter, or the proximal tube of a *Cruziana ancora* type feeding structure (see Seilacher, 1970). The scratch marks seem much too fine to account for the deep, well rounded lobes and probably represent repeated travel through the burrow after construction.

Cruziana problematica (Schindewolf, 1921)

plate 22d

=*Isopodichnus problematica* Schindewolf, 1921 (Bromley and Asgaard, 1979)

Diagnosis

Cruziana less than 6 mm in width with coarse, transverse scratch marks on medial lobes only (after Trewin, 1976; Bromley and Asgaard, 1979; Fillion and Pickerill, 1984).

Stratigraphic Range

Cruziana problematica is known from the Lower Cambrian to the Jurassic (Bromley and Asgaard, 1979; Pienkowski, 1985).

Occurrence

Cruziana problematica was found on float in unit 2.

Description

Specimens consist of furrows, 5 mm or less in width, made up of two well rounded lobes separated by a distinct median groove. The lobes are covered with coarse, transverse, scratch marks or ridges, which often curve back in the same direction at both ends.

Discussion

Cruziana problematica, *Cruziana stromnessa*, and *Rusophycus eutendorfensis* are differentiated from other *Cruziana* and *Rusophycus* by their small size, usually less than 10 mm in width (Bromley and Asgaard, 1979). They are usually interpreted to be the work of branchiopods and other small, non-trilobite arthropods. Some authors place all such forms in a separate ichnogenus: *Isopodichnus*, however this practice is not followed in this study (see Ichnogenus *Cruziana*, Ichnotaxonomy).

The ichnotaxonomy of *Cruziana problematica* has been a source of confusion, not withstanding the *Isopodichnus* controversy. Bromley and Asgaard (1979) lumped all *Cruziana* forms of *Isopodichnus* under *Cruziana problematica*. Fillion and Pickerill (1984), however, noted that at least two distinct forms exist within *Cruziana problematica* based on scratch mark patterns. Thus, they split some forms from *Cruziana problematica* and placed them in *Cruziana stromnessa* Trewin, 1976. They retained *Cruziana problematica* for forms with coarse, transverse, unevenly spaced scratch marks while *Cruziana stromnessa* was reinstated for forms with finer, evenly spaced scratch marks (Fillion and Pickerill, 1984).

The larger problem with "*Isopodichnus*" is the morphological similarity of different forms within it to ichnospecies of larger *Cruziana* and *Rusophycus*. Although some forms, such as *Cruziana problematica*, have distinctive scratch marks, many specimens of "*Isopodichnus*" from this study and others (Trewin, 1976; Bromley and Asgaard, 1979) have the same scratch mark patterns and overall structure as a wide variety of other ichnospecies including *Cruziana barbata*, *Cruziana plicata*, *Cruziana* ichnosp. 2, *Rusophycus bilobatum*, *Rusophycus avalonensis*, and *Rusophycus* ichnosp. 3. The only difference between these forms and the "*Isopodichnus*" equivalents is size, reflecting different trace makers, either different taxa or different stages in the life cycle of the same taxa. Therefore, although the author agrees with Fillion and Pickerill (1984) that a thorough revision of *Isopodichnus* is necessary, the aim of this revision should be to unite the different forms of *Isopodichnus* with ichnospecies of *Cruziana* and *Rusophycus* with which they have morphological affinities, and reserve *Cruziana problematica* and *C. stromnessa* for forms which are unique in aspects other than size alone.

In this study, *Cruziana stromnessa* and *C. problematica* form two distinct groups with no intermediate forms. Most specimens of *Cruziana problematica* from this study consist of forms with coarse scratch marks which were slightly C-shaped in plan view. However, some forms consist of straight, transverse scratch marks. These forms are similar, except for size, to specimens of *Cruziana* ichnosp. 4.

Cruziana rugosa d'Orbigny, 1842

plate 21e, f

Diagnosis

Cruziana with one set of lobes covered with sets of short, straight, parallel, near longitudinal scratch marks. The sets span the width of the lobes, approximately 10–12 scratch marks across. Successive sets are separated by near transverse ridges or gaps. (after Seilacher, 1970; Baldwin, 1977a)

Stratigraphic Range

Cruziana rugosa is most common from the Arenig to Llandeilo although it may range into the Tremadoc and the Devonian (Crimes, 1970b, 1975a; Bradshaw, 1981).

Occurrence

Cruziana rugosa was found in unit 2 and on float at Lake O'Hara.

Description

The furrows consist of 5–10 mm high, well rounded lobes separated by a distinct median groove up to 5 mm deep. Scratch marks are short, averaging 5 mm in length, and form sets of parallel, very regularly spaced, nearly longitudinal marks across the lobe width. The number of scratch marks in a set is difficult to ascertain, but is probably greater than 10. These sets are separated by 1–2 mm wide, nearly transverse linear features: grooves in one sample, ridges in the other.

Discussion

Cruziana rugosa consists of well rounded lobes covered by sets of short, parallel, near transverse scratch marks covering the width of the lobe, giving a corrugated appearance (Seilacher, 1970). Marginal ridges may be present (Crimes and Marcos, 1976).

The regular spacing and colinear ends of the scratch mark sets suggest production by a comb-like appendage (Bergström, 1972, 1973). Slight divergences in some *Cruziana rugosa* scratch marks (Seilacher, 1970) can be attributed to slight changes in the orientation of the appendage during the digging stroke rather than to production by a number of independent appendages (Bergström, 1973). The serially arranged telopodites of trilobites could not have been arranged to make these scratches, especially near the median line (Bergström, 1972). Even if they could, it is unlikely that such a degree of regularity could have been achieved in the resultant scratches (Bergström, 1972). Baldwin (1977a) proposed that the scratch marks could have been made by a wide, multiclawed telopodite. Crimes (1975a) and Bergström (1976) consider it much more likely that they were made by the exite branch, since wide, comb-like telopodites are not known from any trilobite appendage reconstruction (Seilacher, 1985; Müller and Walossek, 1987). However, exite branches that could have scraped across the whole width of a trilobite are not known either (B.D.E. Chatterton, pers. comm., 1988). The data base of known trilobite appendages is too small to substantiate either hypothesis.

There are two explanations for the formation of this ichnospecies. One is that the corrugated scratch marks resulted from passive dragging of posterior appendages with digging and propulsion performed by anterior appendages (Crimes, 1975a; Bergström, 1976). The scratch marks from the anterior appendages would be covered up by the dragging appendages (Crimes, 1975a; Bergström, 1976). The corrugation of the exite scratches could be a result of an up and down motion of the posterior appendages, mirroring the motion of the more anterior ones.

Another explanation is that the same appendages provided both the digging and propulsive forces while making the corrugated scratch marks (Bergström, 1973). Each set of scratch marks would represent a short, posteriorly directed digging stroke. Support for this hypothesis comes from *Rusophycus rugosa*, in which the corrugated scratch marks are found along the whole length of the trace, from outer to inner edges. In *Rusophycus rugosa*, the comb-like appendages must have done at least some of the digging, although some other mechanism, such as shovelling with the anterior margin of the cephalon, may have been responsible for the initial excavation. Shovelling with the cephalon may also have assisted with the excavation of *Cruziana rugosa* (Bergström, 1973) although it could not have provided any propulsive force. The arrangement of scratch marks in *R. rugosa* also implies that the comb-like appendage branch was the dominant appendage branch along the whole body length in these trace makers. The short scratch marks suggest that the range of motion of these appendages was limited. Either they were exite branches, restricted in motion by the telopodites, or they were telopodites, restricted in motion by the other telopodites. If the scratch marks were made by the exite fringe, the telopodites must have been extremely reduced and could have been used to sort through detritus dug up by the exites.

Given their regularity, the scratches in *Cruziana rugosa* were probably made by only a few appendages, with the most posterior appendage forming the final mark (Bergström, 1973). Faint overprinting of scratch marks can be sometimes be seen, indicating that a succession of limbs were active, each pair digging slightly deeper than the previous (Bergström, 1973). As such, the force required from each appendage need not have been large.

Cruziana rugosa usually occurs as short, deep furrows, often intergrading with longer, shallower furrows of either *C. furcifera* or *C. goldfussi* (Seilacher, 1970; Kolb and Wolf, 1979; Pickerill *et al.*, 1984; this study). It represents periods of slower, deeper excavation (Baldwin, 1977a), possibly to exploit more nutrient rich areas. The prevalence of short furrows suggests that this was not an efficient means of forward motion.

The common intergradation of *Cruziana furcifera*, *C. goldfussi*, and *C. rugosa* in a large proportion of the total number of occurrences (Kolb and Wolf, 1979; Pickerill *et al.*, 1984) and the distinctive appendage morphology, indicated by the fact that a wide set of spines could scrape the sediment across the full width of the trace maker, suggests that these three ichnospecies were all produced by a particular, although not necessarily monophyletic group of trilobites or other arthropods.

Kolb and Wolf (1979) grouped *Cruziana furcifera*, *C. goldfussi*, *C. torworthi* Crimes, 1975, *Cruziana breadstoni* Crimes, 1975, and *C. barriosi* Baldwin, 1977 under *Cruziana rugosa*. The reasoning for this was that intergradational examples exist between all these forms, indicating that they were made by the same trilobites, and that there is no difference in their stratigraphic distribution (Kolb and Wolf, 1979). Thus, the different ichnospecies are of little use (Kolb and Wolf, 1979). Aside from the fact that these ichnospecies are distinct morphological types, Pickerill *et al.* (1984) claimed that in most areas there are significant differences in the stratigraphic distributions of these ichnospecies. Thus, most authors have not followed Kolb and Wolf's strategy.

Cruziana semiplicata Salter, 1854
plate 24a, b, c

=*Cruziana similis* Billings, 1872 (Bergström, 1976)

Diagnosis

Cruziana with flat inner lobes, bounded by outer lobes and thin marginal ridges. The inner lobes are covered with coarse, straight, oblique, paired to triple scratch marks. The outer lobes are covered with fine, longitudinal brush marks. Outer lobes and marginal ridges may not be present in all specimens. (Seilacher, 1970).

Stratigraphic Range

Cruziana semiplicata is known from deposits of Early Cambrian to Tremadocian age (Seilacher, 1970; Crimes, 1975a; Bergström, 1976).

Occurrence

Specimens of *Cruziana semiplicata* form A were found in subunits 2l, 2o, and 2s, as well as on float at Moraine Lake. Specimens of *C. semiplicata* form B were found on float in lower unit 4. Their position indicated that they must have come from somewhere within that unit.

Description

There are two distinct forms which conform to the diagnosis for this ichnogenus. Form A consists of broad, curving lateral lobes and flat topped medial lobes separated, by a distinct, shallow median groove (plate 24a, b). Widths vary from 70–100 mm and the height varies from 10–20 mm. These dimensions vary in direct proportion to each other, with the width being 4–6 times the height. The medial lobes make up slightly less than half the width. They are covered with coarse, straight, near transverse, and irregularly spaced scratch marks. Each is apparently made up of 2 well spaced elements. The lateral lobes are flat over the medial half and curve down smoothly at the outer edges. They are covered with distinct, straight brush marks at roughly 0–45° from longitudinal. Their regularity and spacing varies considerably between specimens. There are no marginal ridges on any of the specimens. One specimen of *Cruziana semiplicata* form A grades into a *Rusophycus bilobatum* which in turn grades into a *Cruziana* ichnosp. 4 (plate 24a). The *C. semiplicata* and *R. bilobatum* are of similar relief, while the *C.* ichnosp. 4 is much shallower.

Cruziana semiplicata Form B consists of 50–55 mm wide, 5–10 mm high flat topped bilobed furrows with indistinct median grooves (plate 24c). Furrow width remains constant over the 80–100 mm long fragments while the height varies by as much as 5 mm. There are no lateral lobes or marginal ridges evident. Scratch marks are 2–3 mm wide, and made up of two 1 mm separated, equal elements. They are straight, 60–90° from longitudinal and extend across the width of the lobes.

Discussion

Cruziana semiplicata is distinguished by the presence of lateral lobes with fine, near longitudinal scratch marks and marginal ridges, although neither feature is consistently present in all specimens (Seilacher, 1970).

Lateral lobes are found in a small number of *Cruziana* ichnospecies and a smaller number of *Rusophycus* ichnospecies (see Seilacher, 1970). They are usually covered with fine, near longitudinal lineations or fine, oblique to longitudinal scratch marks (Crimes, 1970c, 1975a, 1975b; Seilacher, 1970). In most cases, lateral lobes are presumed to have been caused by the action of the exites, either actively digging or passively dragging in the sediment (Crimes, 1970c, 1975b; Seilacher, 1970; Bergström, 1972, 1973, 1976; figure 8). This presumption is based on three arguments. The lateral lobes are usually distinct from the medial lobes both in the overall form and ornamentation (Seilacher, 1970) and thus, were presumably made by a different appendage branch. The lineations on the lateral lobes are consistent with the comb-like construction of the exite branch found in most trilobite taxa for which appendage the morphology is known (Seilacher, 1970; Bergström, 1972, 1973; Whittington, 1980; Müller and Walossek, 1987). The exites were stiff structures that could have been used to rake sediment (Bergström, 1972; Whittington, 1980).

There are two problems with this theory. The first is that the most logical function for the exites is gas exchange (Bergström, 1973; Whittington, 1980; Whittington and Almond, 1987) and gas exchange structures are typically delicate and unsuitable for dragging or digging in the sediment. Bergström (1972) however, challenged the gas exchange hypothesis, pointing out that the spinose structure of the exites would be unsuitable for such a purpose. Bergström (1972) proposed that gas exchange is more likely to have taken place through the ventral cuticle. Even if the exites were involved with gas exchange, they need not all have been functional gills; some may have been "sclerotized" for use as straining or digging organs (Bergström and Brassel, 1984). Seilacher (1985) noted evidence for front-to-back size differentiation in appendage size and branch proportion from *Rusophycus* where medial lobe scratch marks become less prominent and lateral brush marks become more prominent towards the back of the trace. This supports the possibility of a front-to-back differentiation in the construction and, thus, the function of the exite branches. Therefore, it is possible that the posterior exites were hardened to manipulate sediment, especially as the posterior exites would have probably become too clogged with sediment dug up by the telopodites to be efficient gas exchange organs in burrowing or furrowing trilobites. Evidence from truncation of telopodite scratch marks (Bergström, 1973; see *Cruziana arizonensis* and *C. furcifera*) and the correlation between the presence of lateral lobes and opisthocline furrowing (head up, tail down) (Crimes, 1970c; Seilacher, 1970) indicates that it was the rear appendages that produced lateral lobes.

The second problem is that most of the reconstructions of trilobite appendages have exite branches that could either not have been brought into contact with the sediment at all, or could not have been oriented so as to bring the tips of the exite spines into contact with the sediment (Whittington, 1980; Cisne, 1981; Müller and Walossek, 1987; Whittington and Almond, 1987; figure 7). Almost all of these reconstructions show the exite fringes imbricated above the exites posterior to them (figure 7a$_{ii}$). Thus, being rigid structures, they could not have been rotated back and down (Whittington, 1980; Whittington and Almond, 1987). However, reliable appendage reconstructions are known from only six trilobite taxa (Whittington, 1980; Seilacher, 1985; Whittington and Almond, 1987). Given the variety of appendage morphologies shown by these forms (figure 7), this small database can not realistically be used to challenge the strong ichnofossil evidence that different appendage branches were used to make medial and lateral lobes in *Cruziana*.

Moreover, there are two appendage reconstructions in which the exite branch could have scraped against the sediment. Müller and Walossek (1987) figured cephalic exites, from *Agnostus pisiformis* meraspids, which are long and articulated so that they could have been dragged along the sediment with the spines pointed down (figure 7c). This provides good evidence for the existence of such an exite construction in a general sense, although in the case of *Agnostus pisiformis*, the spines are too long and coarse to have produced lateral lobe brush marks. Bergström (1972) figured *Cryptolithus* appendages with the exite fringe hanging down along the outside of the telopodite (figures 7b, 8). Such a structure could easily have produced lateral lobes as seen in *Cruziana arizonensis* and *C. semiplicata* (figure 8). Whittington (1980) criticised Bergstrom's reconstruction, claiming that the exite branches of *Cryptolithus* were more likely to have been imbricated against the ventral cuticle as in Whittington's (1980) reconstructions of *Olenoides serratus*. However, evidence from *Protichnites* in this study (see *Protichnites* ichnosp., plate 10a) supports Bergstrom's reconstruction in a general sense, although the trace maker of the *Protichnites* specimens in this study was not *Cryptolithus*.

There is also a possible way in which exite fringes similar to those figured in Whittington (1980) could have been brought into contact with the sediment so as to produce *Cruziana* lateral lobes. If the telopodites were curled up under the body the exite fringe would be rotated out so that the spines would point out, back, and slightly down. The exite fringe could then have been rotated out on its axis (up in the sense of the normal orientation of the exite branch) thus bringing the distal spines into contact with the the sediment. This would be easier in the more posterior appendages if Seilacher's (1985) hypothesis of a front-to-back decrease in telopodite size relative to exite size is correct. Dragging of the exite branches is, thus, the most plausible explanation for the formation of most lateral lobes.

The dragging of the exite lobes is generally thought to have been for capturing or filtering food particles, mainly detritus, from the sediment (Bergström, 1972; Whittington, 1980; Whittington and Almond, 1987); and to assist in digging (Bergström, 1976). The former explanation is more likely in the case of long, longitudinal scratch marks as the exites must have been passively dragged in these cases (Crimes, 1975a). Whittington and Almond (1987) claimed that the exites would be poor food filtering devices since there is no mechanism by which they could have transferred food to the ventro-median food groove. They did not believe that the telopodites could have scraped the exites to effect this transfer while the trilobite was in motion. It is possible, however, that the trace makers stopped periodically to clean food particles off the exites. There may also have been a ciliary mechanism for moving trapped food particles, similar to that used by bivalves to move trapped food off the gills (Boardman *et al.*, 1987).

Another possible function for the exites is the generation of currents to clear away sediment dug up by the telopodites (Seilacher, 1970; Whittington, 1980; Whittington and Almond, 1987). This could be done by flapping the exites, it they were flexible to bend into a sine wave shape, or by using imbricated exite fringes as one way valves (figure 11).

While most lateral lobes can be attributed to the action of the exite branches, Crimes (1975a) proposed that in some cases, they could have been formed by the same telopodites that made the medial lobes. Crimes (1975a, figure 5) figured examples of *Cruziana semiplicata* in which the lateral lobes are covered with sets of parallel, oblique scratch marks that overlap with the more transverse medial lobe scratch marks. A small number of lateral and medial lobe scratch marks are continuous with each other. Crimes' explanation for this involves a two part digging stroke by the telopodites. The first part consists of a weakly impressed, obliquely directed stroke with the telopodite held roughly horizontal. This results in the setae along the side of the telopodite scraping along the sediment; producing the lateral lobe scratch marks. The second phase involves a transversely directed flexation of the telopodite. Only those lateral lobe scratch marks produced by the terminal claws of the telopodite could be continuous with a medial lobe scratch mark. Presumably, the function of this modified telopodite stroke is to scrape detritus onto the setae of the telopodites and transfer this to the ventro-median food groove.

An alternate explanation for the obliquely scratch-marked lateral lobes in Crimes' figure is that they were produced by an exite branch that was rigidly attached to the telopodite. Thus, the telopodite and exite branches would have been drawn in together, creating oblique exite scratches. This might create overlapping fields of scratch marks and could result in some coincidental overprinting of scratch marks. Both of these processes are plausible explanations of the overlapping scratch mark pattern seen in Crimes (1975a, figure 5) and examples of *C. semiplicata* form A in this study (plate 24b).

Cruziana semiplicata form A from this study show a range in lateral lobe scratch mark pattern; from longitudinal wisps (plate 24a) to strongly oblique scratch marks that overlap with medial lobe scratch marks (plate 24b). However, all these specimens have the same cross-sectional shape, suggesting that they were produced by the same mechanism. Since the telopodites could not have produced the fine longitudinal wisps, it is likely that all these specimens were caused by dragging of the exite branches. Specimens of *Cruziana semiplicata* form A differed from the specimen assigned to *C. arizonensis* in that there was almost no difference in relief between the medial and lateral lobes and no evidence of lateral lobes cross-cutting medial lobe scratch marks.

Specimens of *Cruziana semiplicata* form B resemble those in photographs of *C. semiplicata* without lateral lobes (Seilacher 1970, plate 1 figure b and c). Under the scheme proposed in this study (see *C. plicata*) these forms would be assigned to *C. plicata*. They were not however, since they matched Seilacher's (1970) photos so closely; the scratch marks were much coarser and more deeply impressed than those of *C. plicata*; and because it is the intention of the author to follow the established ichnotaxonomy as much as possible. Specimens from this study have single and double scratch marks unlike the triple scratch marks of Seilacher's (1970) specimens. However, the author does not consider scratch mark bunching to be reliable ichnotaxonomic features (see Ichnogenus *Cruziana*, Ichnotaxonomy).

Although there seems to be no morphological justification for separating *Cruziana* *arizonensis* and *C. semiplicata* as defined by Seilacher (1970; see *C. arizonensis*), two morphotypes are contained within the ichnotaxon *C. semiplicata*. One morphotype, conforming to most specimens of *C. semiplicata*, consists of wide, flat furrows with little difference in relief between the medial and lateral lobes. The other morphotype is typified by Seilacher's (1970) drawing of *C. arizonensis* where the lateral lobes are much deeper than the medial lobes. There seems little doubt that the difference between the two morphotypes must be a function of behaviour. If the exite branches had normally projected down as far down below the telopodites, as in *C. arizonensis*, the trilobite would have difficulty walking along the sediment surface. It remains to be seen, however, if the intergradation between these two morphotypes is small enough to warrant making them separate ichnospecies.

Cruziana similis was erected for forms of *Cruziana semiplicata* with only poorly developed lateral lobes (Bergström, 1976). Although different size distributions in concurrent populations of the two ichnospecies suggest that each was made by different trilobite taxa (Bergström, 1976), the range of transitional forms makes the use of *Cruziana similis* too impractical to retain it as a separate ichnospecies.

Cruziana semiplicata, *C. plicata*, and *C. arizonensis* are similar in that the medial lobes are wide, flat, and covered with coarse, straight, near transverse scratch marks. In these ichnospecies, the medial lobes must have resulted from the application of propulsive forces rather than excavation of sediment. They differ from *Rusophycus bilobatum* and *Cruziana* ichnosp. 4 in that the scratch marks of the latter are much more closely spaced and form much more rounded lobes in cross-section. This suggests that the primary purpose of the medial lobe scratch marks in *Rusophycus bilobatum* and *Cruziana* ichnosp. 4 was the excavation of sediment, probably for deposit-feeding, rather than propulsion. Specimens of *Cruziana* ichnosp. 2 can also have rounded lobes with strongly impressed scratch marks. These are distinctly spaced however, unlike those in *C.* ichnosp. 4, and are unlikely to have resulted in the efficient excavation of sediment. They are probably the result of a food-searching process where sensory organs on the appendages test for organic particles in the sediment.

Cruziana stromnessa (Trewin, 1976)
plate 22f

=*Isopodichnus stromnessa* Trewin, 1976 (Bromley and Asgaard, 1979)

Diagnosis

Cruziana less than 6 mm in width with medial lobes only and very fine, transverse scratch marks (after Trewin, 1976; Bromley and Asgaard, 1979; Fillion and Pickerill, 1984).

Stratigraphic Range

Cruziana stromnessa is known from the Lower Cambrian to the Jurassic (Bromley and Asgaard, 1979; Pienkowski, 1985).

Occurrence

Cruziana stromnessa was found in subunits 4m, 6a, and 6c, although most were found in subunit 6a.

Descriptions

Specimens consist of 5 mm wide or less furrows made up of two well rounded lobes separated by a distinct median groove. The lobes are covered with near transverse scratch marks spanning the width of the lobes. The scratch marks are distinctly finer than those on specimens assigned to *C. problematica.*

Discussion

Cruziana stromnessa is discussed under *Cruziana problematica.* The scratch mark pattern on these specimens is similar to that on *Rusophycus eutendorfensis* form A.

Cruziana ichnosp. 1

plates 17b; 21a, b, d

Occurrence

Cruziana ichnosp. 1 was found in a dense assemblage from a single horizon in subunit 4w (plate 21a).

Description

Specimens consist of two, flat to well rounded lobes with a prominent median groove. No lateral lobes or marginal ridges are present. Scratch marks are very fine and grouped in low relief bundles of 3–4, about 1–1.5 mm in total width. Bundles and individual scratch marks exhibit slight undulations. The bundles are long, often over 20 mm, and oriented from near longitudinal to near transverse in different specimens, curving back medially in most specimens. Lobe height varies from 1–5 mm between specimens. The width of the furrows varies from 20–30 mm and is constant within specimens. Furrow length varies from 20–60 mm. Higher relief furrows are often connected to specimens of *Rusophycus* ichnosp. 3. The lobes of *C.* ichnosp. 1 taper at either end, except where they join up with *Rusophycus*.

Discussion

The fine, long, finely undulating scratch marks and wide, low relief lobes are similar to *Cruziana furcifera*, except that the scratch marks are bunched into narrow groups. The length of the scratch marks makes it unlikely that they are the result of the propulsive or digging process. The mechanics of formation are probably the same as for *C. furcifera*, in which digging and propulsion are affected by more anterior appendages. This trace probably represents a deposit-feeding behaviour in which detritus is caught up on the exite fringes. The differences in size and scratch mark detail between *C. furcifera* and *C.* ichnosp. 2 are probably due to a different trace maker.

Cruziana ichnosp. 1 occurs on one bedding plane where it is closely associated, and in many cases joined to, specimens of *Rusophycus* ichnosp. 3. Thus, it must represent an alternate feeding mechanism of the same species of trilobite that produced *Rusophycus* ichnosp. 3.

Cruziana ichnosp. 2

plate 22a, b, c

Occurrence

Cruziana ichnosp. 2 was found in subunits 4o to 4t, 6a, and 6c.

Description

There are two distinct forms within this group. However, with the the small sample size available, it was impossible to decide whether or not to separate them into two different ichnospecies. Form A consists of moderate relief, well rounded lobes, separated by a wide median gap (plate 22a, c). The width of the median gap varies, along furrow, in inverse proportion to the height of the lobes. Furrow width varies from 10–20 mm and maximum lobe height from 1–5 mm. Height varies through this range within single furrows while width is constant. Scratch marks span the width of the lobes. They are coarse, transverse, and well and regularly spaced. Each scratch mark is made up of two equal and regularly spaced elements less than 1 mm apart. Form B is similar in all respects to form A except that the scratch marks are oriented 45–60° from longitudinal (plate 22b).

Discussion

The regular spacing of scratch marks in this ichnospecies, with no overprinting of scratch marks, suggests that only a small number of appendages were responsible for its formation. *Cruziana* ichnosp. 2 forms long trackways of short, smoothly intergrading segments of *Diplichnites* form B, *Cruziana* ichnosp. 2 and *Rusophycus bilobatum*. This proves that both the *Cruziana* and *Rusophycus* could be preserved as shallow, open, surface structures. Assuming the trace makers were trilobites, these tracks also indicate that, contrary to Whittington (1980), some trilobites were able to provide both a digging and propulsive force with the same appendages, at least in shallow furrows. There is no indication that any appendages, other than the ones making the scratch marks, were used. The fact that the trace maker was able to provide propulsive force while dragging its appendages across the sediment at right angles to the trend of motion suggests a strongly cohesive substrate.

The distinctly spaced scratch marks in this ichnospecies are unlikely to have resulted in the efficient excavation of sediment. They are probably the result of a food-searching process where sensory organs on the appendages test for organic particles in the sediment. The association of *Cruziana*, *Diplichnites*, and *Rusophycus* suggests use of a complex feeding behaviour (plate 22a, c). The trace maker might have moved quickly over food poor areas, creating *Diplichnites*, furrowed through the marginal areas testing for organic rich detritus or deposit-feeding off diffuse material, thus creating *Cruziana*, and burrowed deeply into the most organic rich deposits to deposit-feed, creating *Rusophycus*.

Cruziana ichnosp. 3

plate 22e

Occurrence

A single specimen of *Cruziana* ichnosp. 3 was found on float at Lake O'Hara.

Description

The specimen consists of a 15 mm wide, 5 mm high track with vertical sides. The lobes are irregular and knobby with coarse, transverse scratch marks over short stretches. They are separated by a low relief gap covered with short, less than 5 mm long, moderately coarse, near transverse markings.

Discussion

This single specimen could not be assigned to any known ichnospecies of *Cruziana*. The coarse scratch marks along the outer lobes resemble telopodite scratch marks. The knobs within the median gap may have been caused by manipulation of the sediment by the coxae as part of a deposit-feeding behaviour.

Cruziana ichnosp. 4

plate 24a, d, e

Occurrence

Cruziana ichnosp. 4 was found in subunits 2o, 4o to 4x, and on float in unit 6 and at Lake O'Hara.

Description

Specimens consist of wide, low to moderate relief, well rounded medial lobes separated by a deep median groove or gap up to 5 mm in width. The dimensions vary considerably from specimen to specimen. Width varies from 25–68 mm and height from 1–13 mm at the midline of the lobes. Width is constant within specimens but height varies by as much as 50%. Scratch marks are coarse, paired, irregularly spaced, and transverse.

Discussion

Cruziana ichnosp. 4 consists of straight, regular furrows without lateral lobes or marginal ridges. The lobes are covered with coarse, near transverse, multiple, unequal scratch marks. *Cruziana* ichnosp. 4 is similar *C. barbata* except that the scratch marks are grouped in two's at most, unlike the groups of 3–4 in *C. barbata*, and are not as densely arranged as those in Seilacher's (1970, figure 7-7) drawing of *C. barbata*. Ethologically, *Cruziana* ichnosp. 4 and *Cruziana barbata* are probably identical (see below). *Cruziana* ichnosp. 4 has much less regular scratch marks than *C. transversa* Landing and Brett, 1987. Specimens of *Cruziana* ichnosp. 4 differ from those of *C.* ichnosp. 2 in the flatter, wider lobes and the irregularity of the scratch marks. The lobes are rounder however, and the scratch marks much closer to transverse than those in specimens of *Cruziana semiplicata* form B.

The dense pattern of scratch marks suggests that this ichnotaxon is the result of a maximised disturbance of the substrate. As such, it is most likely the result of a deposit-feeding process.

Ichnogenus *Didymaulichnus* Young, 1972

=*Fraena* Rouault, 1850 (*Partim*) (Young, 1972)
=*Rouaultia* de Tromelin, 1878 (*Partim*) (Young, 1972)
=*Cruziana rouaultia* Lebesconte, 1883 (Young, 1972)

Type Ichnospecies

Fraena lyelli Rouault, 1850 by subsequent designation of Young, 1972

Diagnosis

Gently curving, moderately deep, smooth, furrow-like trails, which are bisected longitudinally by a narrow median feature of opposite relief. Trails are oriented parallel to bedding, and may overlap and truncate each other. (after Young, 1972)

Stratigraphic Range

Didymaulichnus has been reported from deposits of late Precambrian to Carboniferous age (Häntzschel, 1975; Pickerill *et al.*, 1984), as well as from the late Cretaceous (Vossler *et al.*, in press).

Discussion

Didymaulichnus consists of a smooth bilobate ridge with a narrow, simple, median groove (Young, 1972). It may have thin marginal ridges or bevels and smoothly defined surface features on the lobes (Pickerill *et al.*, 1984). It is interpreted to be the cast of furrowed trails made by soft bodied animals (Young, 1972; Hakes, 1985). The contention that *Didymaulichnus* could also have been made by trilobites (Crimes, 1970c) is discussed below.

Although it is most commonly regarded as a surface trail (Young, 1972; Eagar *et al.*, 1985; Hakes, 1976), Eagar *et al.* (1985) reported specimens that cross-cut casts of sole marks as being indicative of intrastratal emplacement. It may be, however, that these burrows were actually trails that passed through a thin layer of sand that was the casting medium for the sole marks. Eagar *et al.* (1985) stated that these specimens were on the base of thin turbidite sandstones, but did not give the actual thickness of the beds.

Didymaulichnus probably represents a similar behaviour and mechanism of formation to that of *Scolicia* (*sensu* Häntzschel, 1975): locomotion using a single muscular "foot", in the manner of modern gastropods. The difference in cross-sectional shape between the two ichnogenera may be the result of a difference in body shape or muscular arrangement.

Marginal ridges and bevels are probably the result of a shell, or other body part, dragging in the sediment (Young, 1972). Any surface features are probably due to muscle action or the activity of other body parts, such as a proboscis.

Didymaulichnus has been found in rocks of marginal marine (Hakes, 1985) to deep marine environments (Eagar *et al.*, 1985) but is most commonly associated with shallow marine conditions (Eagar *et al.*, 1985). The exact function that the causative behaviour served is unknown. It is unlikely however, that a trace with a high depth to width ratio, such as *Didymaulichnus*, would result from simple locomotion.

Didymaulichnus is differentiated from other bilobate trails on the basis of fine surface details and on the curvature of the trail. *Taphrehelminthopsis* is also a smooth bilobate trail. It was, however, originally diagnosed as having a central thread-like ridge along the median groove and has subsequently been restricted to tightly coiled and meandering bilobate trails (Young, 1972). *Taphrehelminthopsis* can also be distinguished by its wider median gap (Crimes and Anderson, 1985). *Cruziana* differs by the presence of well developed scratch marks across the lobes (Young, 1972; Häntzschel, 1975; Crimes, 1987). *Aulichnites* differs in that it is a positive relief feature on upper bedding surfaces (Crimes, 1987). *Didymaulyponomos* Bradshaw, 1981 is similar to *Didymaulichnus*, but was erected for specimens formed as true burrows rather than surface traces (Bradshaw, 1981). The depth to width ratio is much greater in *Didymaulyponomos* (Bradshaw, 1981).

Crimes (1970c) attributed *Didymaulichnus* (*Rouaultia*) to the activities of trilobites as well as molluscs. The basis for this argument was that his specimens of *Rouaultia* and *Cruziana*, from a locality in north Wales, had a similar range in width and frequency of marginal ridges, and that the *Rouaultia* often had faint scratch marks. However, his specimens of *Rouaultia* are, in fact, *Cruziana*, in which the scratch marks have not been preserved, perhaps due to poor sediment consistency (Crimes, 1970c). Since preservational variations are not ichnotaxonomically significant (Pemberton and Frey, 1982), these forms should be described as ?*Cruziana* rather than as *Rouaultia*. If there is good evidence that a trace fossil is a preservational variant of a certain ichnotaxon, it should be tentatively assigned to that ichnotaxon rather than to another ichnotaxon to whose diagnosis it may be more similar on the basis of intrinsic morphology alone. *Didymaulichnus* is interpreted to be trails that were emplaced using soft tissue alone, as implied by Young (1972), not using articulated appendages. Thus the contention that *Didymaulichnus* could have been produced by trilobites (Crimes, 1970c; Häntzschel, 1975) cannot be supported. Bradshaw (1981), attributed *Didymaulyponomos* to the activities of arthropods. This would make *Didymaulyponomos* essentially the same as Crimes' *Rouaultia* and, as such, it should be a junior synonym of *Cruziana* since it probably shares the same mechanism of formation.

Didymaulichnus lyelli (Rouault, 1850)
plate 20a, b, c, d

Diagnosis

Smooth surfaced, bilobed ridges without marginal features (after Häntzschel, 1975).

Occurrence

Didymaulichnus lyelli was found in subunits 2o, 4m, 4r, 4w, 4x, 4y, and on float blocks at Moraine Lake.

Description

Specimens consist of smooth, bilobed ridges. There are two distinct size classes: 5 mm wide and 10 mm wide. The 5 mm class consists of 3–5 mm high, steep sided, straight to tortuous tracks that often form dense, overcrossing patterns (plate 20c, d). Height and width vary slightly along the tracks with frequent sharp, shallow constrictions. Track lengths frequently exceed 300 mm. The 10 mm size class consists of 2–4 mm high, short, straight to curved tracks with wide median grooves (plate 20a, b). Faint transverse ribbing can sometimes be observed. One specimen of the 10 mm tracks changes morphology as it passes over another trail; the upper surface becomes broad and flat with 1 mm high marginal ridges (plate 20b). Both size classes are most frequently preserved as convex hypichnia on basal quartzite bedding surfaces. Concave epichnial preservation is much less common.

Discussion

The morphology and dimensions of both of the size classes are within the ranges reported in the literature (Young, 1972; Bradshaw, 1981; Pickerill *et al.*, 1984). The fact that there are two distinct size classes indicates that there were at least two different types of animal making these traces within the same area and time span.

The canted turn with its morphological change, seen in one occurrence of the 10 mm size class, has not been reported before. It suggests that there was a substantial change in muscle action involved in passing over depressions, such as other trails. It also suggests that the bilobed shape of the trace reflects the configuration of the soft tissue during locomotion rather than reflecting any permanent anatomical feature of the trace maker.

Ichnogenus *Diplichnites* Dawson, 1873

?=*Incifex* Dahmer, 1937

Type Ichnospecies
Diplichnites aenigma Dawson, 1873

Diagnosis

Tracks consisting of two roughly parallel series of scratch marks separated by a relatively featureless median gap. Scratch marks are oriented transverse to oblique with respect to the trend of the track and are not associated with a lobe structure. Scratch marks may be single or grouped. (after Häntzschel, 1975)

Stratigraphic Range

Diplichnites has been found in rocks of Early Cambrian to Triassic age (Young, 1972; Häntzschel, 1975; Fillion and Pickerill, 1984).

Discussion

Diplichnites consists of a double row of scratch-like marks separated by a featureless median gap (Häntzschel, 1975). The scratch marks vary from single to composite and normal to oblique with respect to the trend of the trail. They are usually symmetrical across the median gap but may have a marked asymmetry with respect to both orientation and general morphology (Osgood, 1970). *Diplichnites* often merges with *Cruziana*, *Dimorphichnus*, and *Rusophycus* (Crimes, 1970c; Osgood and Drennen, 1975; Baldwin, 1977a) and many forms are transitional with *Cruziana* (Crimes, 1970c). In this study, *Cruziana* and *Diplichnites* were differentiated by the presence of well defined lobes in the former, expressed as a distinct vertical curvature in the scratch marks and significant relief between scratch marks relative to the surrounding sediment surface.

Diplichnites is interpreted to be a surface walking or striding trace of arthropods or other animals with movable appendages (Crimes, 1970c; Osgood and Drennen, 1975; Alpert, 1976; Seilacher, 1985; figure 9). The trace maker moved by scraping its appendages across the sediment surface while applying the propulsive force (Crimes, 1970c). Trilobites used waves of appendage movements propagating from back to front (Seilacher, 1955; Osgood and Drennen, 1975). However, in many cases of both trilobite and non trilobite generated traces, only a small number of appendages must have been used since scratch marks are distinct and well separated (Osgood, 1970). There is no furrow excavated during this behaviour as there is with *Cruziana* (Crimes, 1970c). Asymmetrical

Diplichnites are interpreted to be the result of the trace maker moving obliquely to its body axis, similar to the movement of modern crabs (Osgood, 1970). While most oblique movement is assumed to have been voluntary, walking along a slope or in a crosswise current could also induce oblique walking (Osgood, 1970). In extremely oblique *Diplichnites* (15–30°) the appendage impressions of the trailing side separate out into colinear sets corresponding in number to the number of appendages used (Osgood, 1970).

The direction of movement of the trace maker can be determined in two ways. The most reliable is by the presence of withdrawal markings, mounds of sediment left behind as the appendage is removed from the sediment. With oblique scratch marks the direction of motion is towards the opposite end of the scratch mark from the withdrawal mark (Osgood and Drennen, 1975). The other method is to assume that the V-shaped marks made by oblique scratch marks open out in the direction of travel (Osgood, 1970). There is good evidence supporting this assumption in *Cruziana* and so it is reasonable to assume that the same applies for *Diplichnites*. However, this rule does not hold true for many non-trilobite produced *Diplichnites*, as shown by withdrawal marks (Osgood, 1970).

Crimes (1970c) listed two methods by which the relative speed of travel can be determined for *Diplichnites* (figure 9). Shorter scratch marks suggest a shorter time of contact between appendage and sediment and a quicker stride. Greater separations between successive scratch marks suggest a greater stride length combined with a smaller number of appendages used. Thus, the speed of travel should be inversely proportional to the scratch mark length and directly proportional to the distance between successive scratch marks (Crimes, 1970c).

Diplichnites has no particular physical environmental associations except for current energies low enough to allow the trace maker to remain exposed while the trace is made (see Crimes, 1970c). *Diplichnites* has only been found in deposits of fully marine environments (Baldwin, 1977a). It is most common from shallow marine, subtidal, and mixed and sand dominated intertidal deposits (Baldwin, 1977a; Crimes *et al.*, 1977; Fillion and Pickerill; 1984; Legg, 1985) but has also been found in deep water deposits (Fillion and Pickerill, 1984).

The taxonomy of *Diplichnites*, as well as shallow arthropod surface tracks in general, is in a state of great confusion with no recent taxonomic reviews or monographs (Osgood and Drennen, 1975; Fillion and Pickerill, 1984). There are three surface crawling trace ichnogenera in common use: *Dimorphichnus* Seilacher, 1955; *Diplichnites*; and *Protichnites* Owen, 1852 (Bergström, 1973). However a large number of other ichnogenera are also in use (see Osgood, 1970; Bergström, 1973; Osgood and Drennen, 1975; and synonymies list for *Diplichnites* and *Protichnites* in this paper). Most of these ichnogenera are differentiated on the basis of different inferred trace makers, determined from the number of imprints per set and the shape of the imprints (see Osgood, 1970; Häntzschel, 1975). The author agrees with Bergström (1973) and Bromley and Asgaard (1979) that all arthropod generated surface tracks can be grouped into the three common ichnogenera. However, the currently accepted system groups two ethologically distinct forms under *Diplichnites*: traces where appendages were scraped across the sediment and those in which they were held in place against the sediment (see Osgood and Drennen, 1975), while it restricts *Protichnites* to traces with median drag marks. It is the opinion of the author that this is a seriously flawed system since it lumps ethologically and morphologically distinct forms. The presence of a median drag mark is not a significant feature to either the ethology or the identification of the trace maker of a trace fossil since even a damaged pygidium could cause a drag mark where one would not normally be present.

The following is a proposed taxonomic system that would remain fairly true to the current usage of the three common ichnogenera. *Protichnites* would be restricted to trackways where the appendages remained anchored in the sediment as the propulsive force is applied. In this case, no significant scratch marks would be formed, just impressions corresponding more or less to the shape of the trace maker's appendage with minor scratching on placement or lifting of the appendage. *Diplichnites* would be restricted to forms where the appendages were scraped across the sediment surface as the propulsive force was applied, resulting in long scratch marks. Both *Protichnites* and *Diplichnites* would apply to specimens in which the trace maker moved straight ahead or obliquely. *Dimorphichnus* would be restricted to forms where the movement was so oblique that only the appendages on the leading side provided any propulsive force and those on the trailing side dragged along the sediment (see Ichnogenus *Monomorphichnus*). It is distinct from oblique *Diplichnites* in that both the markings of leading and trailing side appendages separate into sets corresponding to the number of appendages used (Osgood, 1970) This usage of *Dimorphichnus* remains consistent with current usage with the exception that *Allocotichnus* Osgood, 1970 would become a junior synonym of *Dimorphichnus*, rather than of *Diplichnites*, as proposed by Osgood (1970).

The most important feature of this taxonomic strategy is that it separates out ethologically distinct groups. It also avoids the pitfalls of splitting ichnogenera by inferred trace maker, an unreliable process at best since scratch mark patterns may not reflect appendage claw patterns accurately and the number of appendage impressions per set may not reflect the total number of appendages processed by the trace maker (Osgood, 1970; Osgood and Drennen, 1975). Due to the taxonomic confusion surrounding these trace fossils, the author has followed the example of others (Osgood and Drennen, 1975; Fillion and Pickerill, 1984) in not assigning specimens to formal ichnospecies. The specimens described in this study were placed in five natural groups based on relationships in scratch mark orientation, symmetry, and strength of impression. As all five forms intergrade, they were probably produced by the same group, or groups of trace makers

Diplichnites form A
plates 17e; 18a, c, f

Occurrence

Diplichnites form A was found in subunits 2b, 21, 4r, 4t, 4x, and 6e, as well as on float at Lake O'Hara and Moraine Lake.

Description

These trackways consist of two bands of scratch marks separated by a featureless median gap. The scratch marks are symmetrical across the median gap, transverse to oblique, short, well spaced, and either single or paired with distinct spaces between pair elements. The scratch mark bands have no lobe structure. In one specimen, this form of *Diplichnites* was seen to grade into *Diplichnites* forms B and D (plate 17e).

Discussion

This form is indicative of straight forward movement utilising a small number of limbs resulting in well spaced, distinct scratch marks. The fine scratch marks suggest that the appendages were not firmly impressed into the sediment. This and the shortness of the scratch marks suggest a fairly rapid rate of progress (Crimes, 1970c). *Diplichnites* form A is probably the result of simple locomotion. Many of the single, transversely scratch marked forms conform to the diagnosis of *Incifex*.

Diplichnites form B
plates 17a; 18b, d

Occurrence

Diplichnites form B was found in subunits 2b, 21, 4s, 4t, 6a, 6c, and 6e and on float at Lake O'Hara and Moraine Lake.

Description

These trackways consist of two bands of scratch marks separated by a featureless median gap. The scratch marks are symmetrical across the median gap and are short, near transverse, and composed of irregularly bunched, deeply impressed, multiple elements. Scratch mark bunches are distinctly but irregularly spaced. Scratch marks have a definite relief consisting of a concave down, vertical curvature.

Discussion

Diplichnites form B differs from *D.* form A in that the scratch marks are longer, coarser, and are composed of a number of irregularly spaced elements. This suggests that either the appendages were more deeply impressed into the sediment or, far less likely, a number of successive appendages moved across the same grooves. The former explanation is indicative of a slower rate of progress than form A, a less cohesive substrate, or both. The deeply impressed scratch marks suggest that this ichnotaxon is not the result of simple locomotion but perhaps caused by a deposit-feeding or food-searching behaviour (see *Cruziana* ichnosp. 2).

The scratch mark pattern of *Diplichnites* forms A and B also indicate that the trace makers were able to provide a forward propulsive force while dragging their appendages across the sediment surface at right angles to the direction of motion since there is no evidence for the action of any other appendages. This should only be possible on a sufficiently cohesive substrate, to prevent backwards slippage of the appendage tips.

The scratch mark pattern of *Diplichnites* form B is very similar to that of *Cruziana* ichnosp. 4 and *Rusophycus bilobatum*, and several specimens are transitional with these ichnospecies indicating that the same trilobites were responsible for all three forms. *Diplichnites* form B also forms a component of long trackways consisting of short intergrading segments of *Diplichnites*, *Cruziana* ichnosp. 2 and *Rusophycus bilobatum*. The ethological significance of this is discussed under *Cruziana* ichnosp. 2.

Diplichnites form C

Occurrence

Diplichnites form C was found in subunits 2q, 4s, and 6c, and on float at Moraine Lake.

Description

These trackways consist of two bands of scratch marks separated by a featureless median gap. The scratch marks are symmetrical across the median gap and are short, oblique, and irregularly spaced and oriented. There is no lobe structure.

Discussion

This form is distinct from forms A and B in the irregularity of the spacing and orientation of the scratch marks.

Diplichnites form D
plates 17c, e; 19a

Occurrence

Diplichnites form D was found in subunit 4w and on float at Lake O'Hara and Moraine Lake.

Description

These trackways are similar to *Diplichnites*, form A, except that there is a marked asymmetry in scratch mark strength, orientation, and curvature across the median gap.

Discussion

The mechanics of formation (strength of appendage impression, stride length, speed of motion) inferred for form D is similar to form A except that the trace maker moved obliquely with respect to its body axis, rather than straight ahead.

Diplichnites form E
plates 17a; 19c

Occurrence

Diplichnites form E was found on float in subunit 6d and at Moraine Lake.

Description

These trackways are similar to *Diplichnites* form B, except that the scratch marks are more oblique and are subparallel with those on the opposite lobe rather than being mirror images of each other.

Discussion

The mechanics of formation inferred for *Diplichnites* form E is similar to *D.* form B except that the trace maker moved obliquely with respect to its body axis.

This form of *Diplichnites* was found grading into trackways of *Diplichnites* form B at changes in trackway orientation (plate 17e). This change in scratch mark pattern suggests the trace maker changed its orientation with respect to water currents when it changed direction. One short specimen of *Diplichnites* form E intergrades with *Monomorphichnus* at both ends (plate 19c). This suggests that the trace maker dropped down onto the sediment to investigate a potentially favourable feeding area, encountered while searching with the *Monomorphichnus* behaviour (see *Monomorphichnus*).

Ichnogenus *Diplocraterion* Torell, 1870

Type Ichnospecies

Diplocraterion parallelum Torell, 1870, by subsequent designation of Richter, 1962

Diagnosis

Vertical U-shaped tubes with spreiten. Spreiten may be protrusive, retrusive, or both, but never extend laterally beyond the dimensions of the U-tube. Terminations of the tubes may be straight or funnel shaped. (Fürsich, 1974a; Häntzschel, 1975)

Stratigraphic Range

Diplocraterion has been reported in rocks of latest Precambrian to Cretaceous age (Häntzschel, 1975), although it is likely to range into the modern.

Discussion

Diplocraterion is distinguished from other vertical U-shaped burrows by the presence of spreiten and from *Rhizocorallium*, in that the latter is roughly parallel to bedding over most of its length (Fürsich, 1974a). The burrows may be lined or unlined (Fürsich, 1974a). *Diplocraterion* is interpreted to be the dwelling burrow of filter-feeding animals (Osgood, 1970; Fürsich, 1974a). It has been attributed to polychaetes (Chamberlain, 1977) and crustaceans (Runnegar, 1982) although it could be made by almost any small filter-feeding animal (Osgood, 1970).

The contention that the spreiten in *Diplocraterion* may be the result of deposit-feeding is refuted by Fürsich (1974a) since organic rich layers are usually horizontal and the spreiten in *Diplocraterion* are vertical. The most accepted explanation is that the spreiten are the result of the readjustment of burrow depth to maintain an optimum burrow length (see Fürsich, 1974a). Although protrusive spreiten could be caused by accommodations to growth of the trace maker over its life cycle, most spreiten are thought to be the result of responses to erosion and deposition (Fürsich, 1974a). The trace maker moves the burrow up in response to net sediment deposition and down in response to net erosion to keep the burrow depth constant. With a number of burrows, started at different times, a series of erosional and depositional events can be placed in sequence (Goldring, 1962).

Diplocraterion is found in deposits of high energy environments with abundant suspended organic material (Chamberlain, 1977; Crimes, 1977). The very fact that spreiten are found indicates that these environments are erosionally and depositionally unstable to some degree. The presence of burrow linings indicates a poorly cohesive substrate (Fürsich, 1974a).

Diplocraterion has been found in deposits of fluvial and lacustrine environments (Pollard *et al.*, 1982), intertidal and shallow subtidal settings (Chamberlain, 1977; Crimes *et al.*, 1977), and deep water submarine fans (Crimes *et al.*, 1981). It is found in both large, monotaxonomic assemblages (Crimes *et al.*, 1977; Frey and Pemberton, 1984; Clausen and Vilhjalmsson, 1986) and in more diverse assemblages of filter-feeder trace fossils (Crimes and Anderson, 1985).

Diplocraterion parallelum Torell, 1870

plate 12e

Diagnosis

Diplocraterion having parallel burrow walls and unidirectional spreiten (Fürsich, 1974a).

Occurrence

Diplocraterion parallelum was found in subunits 3a, 4h, and on float at Moraine Lake. Uncertain specimens were found in subunits 2q, 4o, and 4w.

Description

Specimens consist of unlined, 5–10 mm diameter U-shaped tubes (plate 12e). Where accurate measurements could be made, width varies from 25–30 mm and height averages 50 mm. All specimens have protrusive spreiten although these are often quite vague. The Moraine Lake specimens are in amalgamated, trough cross-bedded quartzites, with brown shale infill and spreite. The specimens in subunit 3a are in densely burrowed quartzite with a structureless, clean quartzite infill. The specimens in subunit 4h were in soft, sandy shale with a similar infill. The uncertain specimens consist of paired, 3–4 mm diameter, unlined shafts, 10–20 mm apart. These are connected by 2 mm wide, slightly curving band of quartzite with a complex internal structure.

Discussion

The presence of U-shaped tubes with only protrusive spreiten suggests a high frequency of small scale erosional events in the sandstone and mudstone dominated deposits in which they were found (Goldring, 1962). The specimens from Moraine Lake and subunit 3a are likely the result of filter-feeders given the clean sand and lack of deposit-feeding infauna. Those from subunit 4h are more likely the result of surface deposit-feeders as the quiet water conditions implied by the muddy substrate would not have suspended sufficient quantities of food material for filter-feeding..

The quartzite bands connecting these paired shafts of the uncertain specimens are interpreted to be spreiten. However, no confident ichnospecific assignment can be made without side views (Crimes *et al.*, 1977). These structures indicate the occurrence of small scale erosional events in units 2 and 4 (Goldring, 1962).

Ichnogenus *Dolopichnus* Alpert and Moore, 1975

Type Ichnospecies

Dolopichnus gulosus Alpert and Moore, 1975

Diagnosis

Vertical, cylindrical burrows with a narrower, central cylindrical core that may terminate in an indistinct bulbous enlargement. (Pemberton *et al.*, 1988)

Stratigraphic Range

Dolopichnus is known mostly from the Lower Cambrian, although Mesozoic material including *Laevicyclus mangraensis* may prove to be synonymous (Alpert and Moore, 1975; Pemberton *et al.*, 1988).

Discussion

Like *Bergaueria*, *Dolopichnus* is interpreted to be the cast of sea anemone burrows (Alpert and Moore, 1975). It is similar in shape to *Bergaueria*, except for the central axial cylinder; the higher height to diameter ratios (4:1) in complete specimens; and the bulbous terminations, interpreted to be made by the trace maker's physa (Pemberton *et al.*, 1988). They are also similar to *Bergaueria* with respect to the mode and inferred mechanisms of preservation (see Ichnogenus *Bergaueria*; Alpert and Moore, 1975).

Ethologically, *Dolopichnus* and *Bergaueria* are subtly different. *Dolopichnus* is frequently found with trilobite fragments within the central cylinder (Alpert and Moore, 1975), thus, the trace makers may have specialised on larger prey organisms. According to Alpert and Moore (1975), sea anemones will collect skeletal material into mucus bound cylinders to facilitate expulsion. This material would be pressed against the side of the central cylinder in Alpert's (1973) mechanism of preservation (see below).

The elongate shape of *Dolopichnus* suggests that it was made by cerianthid anemones rather than actinarian anemones which were responsible for *Bergaueria* (Alpert, 1973; Barnes, 1980). Cerianthid anemones are elongate, typically soft ground burrowers that reinforce their burrows with thick linings of mucus, fired nematocysts, and related organelles (Barnes, 1980). Infilling of this thickly lined pit (in the manner of *Bergaueria*) is a more plausible explanation for the double cylinder structure of *Dolopichnus* than Alpert and Moore's (1975) differential infilling of the anemone's coelenteron and surrounding burrow (see Pemberton *et al.*, 1988) or compaction of the surrounding sediment by expansion and contraction of the anenome's coelenteron (Pemberton *et al.*, 1988) given the distinct margins of the outer cylinder. The only problem with this explanation is that many examples of *Dolopichnus*, including those from this study, are found in shale and yet the outer zone is composed of sand. The *Dolopichnus* making animal must have selectively packed the lining with coarse material to make the mucus bound lining theory possible.

The mechanism of formation for *Dolopichnus* is much more complex then the simple pit of most *Bergaueria*. However, the general ethological implications are similar, thus, the implied gross environmental constraints are similar as well. *Dolopichnus* trace makers may have been better suited to softer substrates as a result of the thicker lining.

?*Dolopichnus*

plate 7d, e, f

Occurrence

?*Dolopichnus* was found on float in unit 4 and at Lake O'Hara. In neither case was it possible to trace the float blocks to a particular stratigraphic position.

Description

Specimens consist of straight sided, vertical burrows with circular cross-sections. The outer diameter of the burrows averages 44 mm ± 5 mm. The diameter of the central core averages 16 mm. There is appears to be a thin, dark lining separating the inner cylinder and outer layer. The exposed height of complete specimens varies from 20–25 mm. The outer layer slopes towards the central core over the lower 5–10 mm of the burrows, with the central cylinder sticking out by up to 5 mm. In many cases however, this may be due to abrasion of the outer lining. There is no evidence for ornamentation in any of the samples. The infill of both zones consists of grey quartzite, similar to the overlying rock. The surrounding rock is shale.

The specimens from the Lake O'Hara float block are separated by 7–38 mm with an average of 22 mm (plate 7d). Those on the Redoubt Mountain float block are separated by 3–10 mm with an average of 6 mm (plate 7e, f). There is no obvious pattern to the spatial distribution in either case.

Discussion

These samples differ from descriptions in the literature in that the height to diameter ratio is close to 1. This may be due either to erosional truncation of the burrows at the top, abrasion of the bottom after exposure, a combination of both, or a difference in the trace making animal from other occurrences in the literature. Differential abrasion of the outer and inner cylinder suggests a different composition. This supports the hypothesis that the outer cylinder is a biologically constructed lining while the inner cylinder is a passively infilled burrow.

Ichnogenus *Gordia* Emmons, 1844

Type Ichnospecies

Gordia marina Emmons, 1844

Diagnosis

Smooth, non-branching burrows, of uniform diameter, forming irregular, smooth curves and loops with frequent level overcrossings (after Häntzschel, 1975).

Stratigraphic Range

Gordia has been reported in deposits of latest Precambrian to Cenozoic age (Häntzschel, 1975).

Discussion

Gordia consists of smooth burrows, of constant diameter within specimens, that loop and curve irregularly forming complexly intertwining patterns with frequent level overcrossings and little vertical displacement of burrows (Häntzschel, 1975). The burrow diameters are typically 0.3–4.0 mm (Häntzschel, 1975).

Gordia has been found in a wide variety of sedimentary settings (Ratcliffe and Fagerstrom, 1980). It most likely represents the utilisation of a small area of organic rich sediment by an infaunal deposit-feeder (Chamberlain, 1977). This behaviour is different from many other such strategies in that there is no apparent organisation to the burrows that would reflect an attempt at maximisation of feeding efficiency. This suggests a lack of competition for food or space. *Gordia* has been attributed to polychaetes (Chamberlain, 1977).

Gordia is distinguished from *Planolites* by its smaller diameter and its complex, vertically restricted patterns (see Häntzschel, 1975). Recognition is difficult in many specimens, however, since it depends on the recognition of gross patterns which may not be seen on small fragments or in well bioturbated settings.

Gordia marina Emmons, 1844
plate 10d

Diagnosis

Gordia with a diameter greater than 0.4 mm (Ksiazkiewicz, 1977).

Occurrence

Gordia marina was found in subunits 2i, 2m, 2o, 2s, 4o, and 6c.

Description

Specimens consist of smooth, irregularly curving and looping, unlined, quartzite infilled burrows on the base of thick quartzite beds. Burrow diameters vary from 1–3 mm. Specimens usually occur in the absence of other ichnogenera.

Discussion

The interpretation of this ichnospecies is essentially the same as that of the ichnogenus as a whole. Ichnospecific differences appear to reflect taxonomic differences in the trace maker rather than differences in the causative behaviour or environmental influences. The fact that these specimens usually occur alone and are of a highly disorganised nature suggests that they were made by animals that were adapted to conditions that excluded other infauna, and thus had no need to optimise their foraging pattern due to a lack of competition for food.

Ichnogenus *Monomorphichnus* Crimes, 1970c

Type Ichnospecies

Monomorphichnus bilinearis Crimes, 1970c

Diagnosis

Sets of parallel to subparallel, straight to sinusoidal scratch-like ridges which may be of unequal length and have longitudinally offset terminations. Each scratch mark may be made up of a number of finer scratch marks. Sets of scratch marks are often repeated at intervals, usually with a lateral offset between sets with respect to the trend of the scratch marks. (after Crimes, 1970c; Häntzschel, 1975)

Stratigraphic Range

Monomorphichnus has been reported from deposits of Early Cambrian (Alpert, 1976; Crimes and Anderson, 1985; Fritz and Crimes, 1985) to Triassic age (Shone, 1979).

Discussion

Monomorphichnus consists of sets of short, fine, roughly parallel ridges (Crimes, 1970c). Individual ridges may be single or consist close spaced groups within the set. They vary from straight to sigmoidally curved. They may be of equal length across a set or vary in length, either irregularly or systematically within the set. These sets usually form serially repeating trails, often with slight lateral offsets (Crimes, 1970c). *Monomorphichnus* differs from *Dimorphichnus* in that the later has short, blunt ridges along one end of each set of longer ridges (Crimes, 1970c).

Monomorphichnus is interpreted to be the cast of traces made by trilobites, or other arthropods, moving sideways through the water just above the sediment surface and periodically dragging the trailing side appendages along the sediment surface (Crimes, 1970c, 1987; figure 9). The trace maker may have actively swum or been carried by currents. *Dimorphichnus* carries a similar interpretation except the trace maker pulled itself along with the leading side appendages, leaving the blunt impressions as well as the long grooves (Crimes, 1970c; figure 9). Traces similar to *Dimorphichnus* are produced by modern arthropods (Crimes, 1970c).

The ethological interpretation of *Monomorphichnus* and *Dimorphichnus* is the source of some controversy (Osgood, 1970, 1975). Crimes (1970c; Crimes and Anderson, 1985) maintained that *Monomorphichnus* is the result of a surface deposit-feeding behaviour whereby the trace maker raked up detritus from the sediment surface with the trailing side appendages. Osgood (1970, 1975) however, claimed that this would be a very inefficient means of feeding since there is no documented means of transferring food particles efficiently from the appendages to the mouth. According to Osgood (1975) it is just as likely that these two ichnotaxa represent animals caught up in water currents and raking against the sediment in an effort to control themselves or regain their position on the bottom. Banks (1970) stated that some *Monomorphichnus* may be the result of dead trilobites carried by currents. Some *Monomorphichnus* may in fact represent such out of control animals, however, most *Monomorphichnus* are found in interbedded shales and siltstones with no evidence for strong currents (Crimes, 1970c). Moreover, many examples display a regularity in the length and spacing of sets that suggest an animal very much in control of its actions.

Osgood's (1975) criticism about the transport of food from the legs to the mouth can be handled in two ways. Contrary to Osgood (1975), food particles scraped off the sediment could have been transported to the ventro-median food groove (see ichnogenus *Cruziana* and Ichnogenus *Rusophycus*) on the terminal setae of the telopodites. The other possibility is that *Monomorphichnus* results from a food-searching behaviour. The periodic raking of the sediment involved in the production of *Monomorphichnus* could have resulted from the periodic testing of the substrate for detritus rich areas. Once such an area was found, the trace maker could drop down onto the sediment to feed (plate 19c, *Diplichnites* form E).

Monomorphichnus is found in a wide variety of sedimentary facies but is most common in deposits indicative of quiet water, consisting of thinly-bedded sandstones, siltstones, and shales (Crimes, 1970c). This could be the result of the low preservation potential for shallow surface traces in high energy environments, however, Crimes (1970c) noted a decrease in the abundance of *Cruziana* in such quiet water deposits. This would not be expected on the basis of preservation potential. Thus, there must be a real shift from deep furrowing traces to shallower surface traces in quiet water (Crimes, 1970c). This would be expected in a surface deposit-feeding behaviour. *Monomorphichnus* displaying a high degree of regularity should be indicative of quiet water where organic detritus can accumulate on the bottom and small surface dwelling animals can flourish. Irregular *Monomorphichnus* with long scratch marks are indicative of periodic currents which carried the trace makers along out of control, but were not strong enough to erode the traces. *Monomorphichnus* is generally found in deposits of shallow marine, mixed and sand dominated intertidal flat, and tidal channel environments (Baldwin, 1977a; Legg, 1985). It has also been reported from estuarine (Fisher, 1978) and fluvial deposits (Shone, 1979).

Monomorphichnus, as well as many other surface emplaced traces, are important indicators of normal, or background current conditions rather than those responsible for the deposition of the casting medium. Cross-cutting and intergrading relationships between these and other traces are useful in distinguishing between burrow-like surface trails and true burrows.

With the exception of *Monomorphichnus multilineatus* Alpert 1976, most ichnospecies of *Monomorphichnus* are differentiated by different scratch mark patterns (see Crimes, 1970c; Crimes *et al.*, 1977; Legg, 1985) with the assumption being that this is an indication of claw patterns, and thus the identity of the trace maker (Crimes, 1970c). There are several reasons why this is a questionable practice. Given a certain claw pattern, the number, shape, and spacing of ridges making up one element of a *Monomorphichnus* set can vary with a number of conditions (Osgood, 1970; Osgood and Drennen, 1975; Crimes *et al.*, 1977). These include the angle at which the end of the appendage strikes the sediment, the angle between the direction of movement and the axis of the limb, the force or depth of impression, and the consistency of the sediment (see Seilacher, 1962, figure 2). Moreover, there is almost no evidence to determine the relationship between trilobite taxonomy and appendicular claw patterns (Whittington, 1980; G. Edgecombe, pers. comm., 1987). Thus, differentiating ichnospecies of *Monomorphichnus* by scratch mark pattern is without any real significance, either morphological or ethological, except convenience.

The following morphologic features are likely to be of ethological and environmental significance and may be more appropriate ichnospecific features. Scratch mark relief is proportional to the force of impression and sediment consistency. Scratch mark length and spacing between sets is probably proportional to the speed of movement (see Crimes, 1970c). Variations in scratch mark length within a set and longitudinal offsets within a set indicate that the appendages were not set down or taken up in unison. Consistent longitudinal offsets suggest that the trace maker was not moving at exactly a right angle to its body axis. The degree of regularity in set morphology and spacing may be proportional to the degree of control the animal had over its actions. The spacing of elements within a set may also have some ethological significance although it is more likely to depend on trace maker morphology. Specimens in this study were not classified into any of the recognised ichnospecies of *Monomorphichnus*. Instead, They were grouped informally based on the above features.

Monomorphichnus is easily overlooked on heavily bioturbated surfaces since only a small section of a few scratches may be visible. Thus, the abundance of *Monomorphichnus* in well bioturbated zones was probably underestimated in this study.

Monomorphichnus form A

plate 19b, c, e

Occurrence

Monomorphichnus form A was found in subunits 4r, 4s, 6a, and 6c, as well as on float at Moraine Lake and Lake O'Hara.

Description

Specimens consist of serially arranged sets of scratch marks with independently varying lateral and longitudinal offsets of 10–50 mm between sets. Sets are made up of 4–10 parallel scratch marks, 5–80 mm long and less than 10 mm apart. The median marks are the longest. Scratch marks are either single or paired and are generally straight, although some have a slight curve at one end. Length and spacing of scratch marks varies slightly from set to set. Some specimens occur in dense patterns of randomly oriented scratch mark sets. One specimen of *Monomorphichnus* form A had a short stretch of *Diplichnites* form E incorporated into the *Monomorphichnus* trackway (plate 19c).

Discussion

The straightness of the serial tracks suggests a purposeful behaviour rather than an out of control animal. Thus, this form most likely represents a surface deposit-feeding or food-searching behaviour. The dense horizons of randomly oriented sets are probably the result of a number of trace makers feeding off an organic rich surface. *Monomorphichnus* intergrading with *Diplichnites* indicates an interruption of the swimming activity, either to investigate a potential food source or to rest. *Monomorphichnus* form A could have been assigned to *Monomorphichnus multilineatus* based on the increase in scratch mark length towards the middle of each set (Alpert, 1976).

Monomorphichnus form B

plates 19d; 20e

Occurrence

Monomorphichnus form B was found in subunits 2l, 2q, 4r, 4t, 4v, 4w, 6a, 6c, as well as on float at Moraine Lake and Lake O'Hara.

Description

Specimens consist of isolated sets of 5–10, 5–30 mm long, near parallel, widely spaced scratch marks. There is a consistent lateral offset of approximately half a scratch mark length successive scratch marks across a set. Scratch marks often increase in length towards one side of the set. Sets are serially arranged with lateral offsets less than one set width.

Discussion

The large longitudinal offset suggests that the trace maker was moving at an angle less than 90° to the long axis of its body. The extremely short scratch marks relative to the width of the sets is not consistent with a deposit-feeding behaviour since it suggests that the appendages spent only a small amount of time in contact with the sediment. It is more likely that this form represents either current assisted locomotion in which appendage dragging was used to control the animal or a food-searching behaviour in which the trace maker tested the substrate periodically as it moved along. This form could have been assigned to *Monomorphichnus lineatus* given the single scratch marks (Crimes *et al.*, 1977).

Monomorphichnus form C

plate 19b, f

Occurrence

Monomorphichnus form C was found on float at Moraine Lake and Lake O'Hara.

Description

Specimens consist of isolated *Monomorphichnus* sets that have irregular, subparallel to strongly convergent scratch marks with angular differences of up to 15° across a set.

Discussion

The convergent scratch marks suggest an animal scooping material off the sediment surface. This is consistent with a surface deposit-feeding activity.

Monomorphichnus form D

plate 20f

Occurrence

Monomorphichnus form D was found on float at Moraine Lake.

Description

Specimens consist of closely spaced, long, multiple, clumped scratch marks, similar to *Diplichnites* form D. They form sets of subparallel, unequal length marks. The sets form long, curving tracks with almost no lateral offset between sets.

Discussion

The irregular curving appearance and long scratch marks of this form suggest an animal carried along out of control by strong currents.

Ichnogenus *Palaeophycus* Hall, 1847

Type Ichnospecies

Palaeophycus tubularis Hall, 1847, by subsequent designation of Bassler, 1915

Diagnosis

Branched or non-branching, smooth or ornamented, lined, essentially cylindrical, predominantly horizontal burrows of variable diameter; infilling is typically structureless, and of the same lithology as the host rock (Pemberton and Frey, 1982).

Stratigraphic Range

Palaeophycus has been reported in deposits of Precambrian to Holocene age (Häntzschel, 1975).

Discussion

Palaeophycus consists of lined burrows, oriented predominantly horizontal or slightly inclined to bedding, but often having short, near vertical segments. True branching occurs rarely. The infill is essentially structureless and of similar lithology to either the host rock or a superjacent rock with which the burrow is in contact at some point. *Palaeophycus* is interpreted to be the remains of open burrows that were passively infilled after abandonment by the trace maker. Collapse features and vertically compressed burrows are common. (Pemberton and Frey, 1982).

Palaeophycus is thought to be the result of the activities of sessile infaunal suspension-feeders and motile, infaunal carnivores, most commonly polychaetes (Pemberton and Frey, 1982). It was either maintained as permanent or semipermanent domichnia or left as open tubes after passage of the trace maker (Pemberton and Frey, 1982). *Palaeophycus* is a eurybathic trace fossil, occurring in a wide range of marine environments (Fillion and Pickerill, 1984). As such it is of limited use in paleoenvironmental reconstructions.

Wall ornamentation reflects the different modes of propulsion used by the trace makers and is one of the attributes used for classifying the various ichnospecies of *Palaeophycus* (Pemberton and Frey, 1982). The thickness of the lining is directly proportional to both the permanence of the structure and the cohesiveness of the substrate. Thick linings are probably specially constructed structures. Thin linings are most likely the result of a thin mucus linings in the original burrow. Such linings facilitate movement of the trace maker. Visible preservation of mucus linings requires adsorption of contrasting sediments by the mucus (see Ichnogenus *Skolithos*).

Palaeophycus heberti (Saporta, 1872)
plate 9c

Diagnosis

Smooth, unornamented, thickly lined, cylindrical burrows (Pemberton and Frey, 1982).

Occurrence

Palaeophycus heberti was found in subunit 4x and on float at Lake O'Hara.

Description

Specimens consist of 5–10 mm diameter horizontal burrows with quartzite linings comprising 15–20% of the burrow diameter. Burrow infill is similar to the host rock, which is quartzite in both occurrences. The burrows are only seen in cross-sectional view so the presence of surface ornamentation and the degree of burrow curvature can not be ascertained.

Discussion

The thick wall lining of this ichnospecies reflects a permanent burrow, perhaps in a poorly cohesive sediment. A burrow that was not maintained after its formation would not have such a well constructed lining since the long term survival of the burrow would not be important.

Palaeophycus striatus Hall, 1852
plate 9b

Diagnosis

Thinly lined burrows covered with fine, continuous, parallel, longitudinal striae (Pemberton and Frey, 1982).

Occurrence

Palaeophycus striatus was found in subunits 2j, 2o, 2q, 4d, 4n, 4o, 4s, 4t, 4w, 5d, 6c, and 6g, as well as on float at Moraine Lake and Lake O'Hara. It is most common at Lake O'Hara.

Description

Specimens consist of 1–6 mm diameter, clean quartzite infilled burrows with indistinct, dark linings less than 1 mm thick. Burrows are of constant diameter along length except for occasional and irregular constrictions, 1–3 mm length. Within a sample, burrows tend to have diameters within 2–3 mm of each other. The outer walls are covered with very fine, longitudinal striae. The delicacy of the striae makes it difficult to determine their longitudinal consistency. Burrows are gently curving in both the horizontal and vertical direction. They are preserved as endichnia and hypichnia on the base of thin, dark shale bounded, brown to white quartzites.

Discussion

Palaeophycus striatus is distinguished by fine, parallel, continuous striae (Pemberton and Frey, 1982). The continuity of the striae suggests that the fine spines that produced them were used as anchoring devices against which the trace maker pushed and were not used to dig or provide propulsive force as were movable appendages in the production other striated burrows such as *Trichophycus*. The fact that most "populations" of burrows are of similar diameter suggests that most groups of burrows were made by the same type of trace maker. The length of the burrows and the thinness of the lining suggests that these burrows were made by motile infauna.

Palaeophycus tubularis Hall, 1847
plate 9a

Diagnosis

Smooth, unornamented, thinly lined burrows of variable diameter (Pemberton and Frey, 1982).

Occurrence

Specimens that can be unequivocally assigned to *Palaeophycus tubularis* were found in subunits 2a, 2b, and 2m. Specimens which are similar, but for which wall lining ornamentation can not be accurately determined were found throughout unit 2 as well as in subunits 3b, 4o, 4r, 4t, 4w, 4x, 4y, 5b, 5d, 6a, and 6c.

Description

Specimens consist of 2–7 mm diameter, quartzite infilled burrows with smooth black linings less than 1 mm thick. Burrows are of constant diameter along length except for frequent 1–3 mm long, irregular constrictions. These constrictions reduce the diameter by up to 50%. Within a sample, burrows tend to have diameters within 2–3 mm of each other. Burrows vary from gently curving in both the horizontal and vertical directions to tortuous and intertwining. Interpenetration is rare. Specimens are preserved as endichnia and hypichnia on the base of thin, dark shale bounded, brown to white quartzites.

Discussion

The thin, smooth lining in these specimens are characteristic of *Palaeophycus tubularis*. The frequency of collapse structures is consistent with the thinness of the wall lining. These features indicate that the burrows were made by mobile infauna in contrast to thickly lined ichnospecies, such as *P. heberti*. This is the most common variety of *Palaeophycus* in this study, probably because most doubtful specimens were assigned to it.

?*Palaeophycus*

plate 12a, c.

Occurrence

?*Palaeophycus* was found in subunits 2b, 2j, 5d, 6c, 6e, and 6g and on float at Lake O'Hara.

Description

Specimens consist of unlined, smooth walled, clean quartzite infilled burrows 3–8 mm in diameter. Specimens from Redoubt Mountain are preserved as endichnia within dark to light brown shales and silty shales. The specimens from Lake O'Hara are preserved on the base of thin, clean quartzites similar to the burrow infill.

One unusual specimen was found at Lake O'Hara. It consists of an 8.5 mm diameter, unlined, white crystalline quartzite infilled burrow, 20 mm long and fragmented at both ends. There are a number of small angle bends over this length. The wall is sharply defined and covered with fine, irregular peristaltic-like annulations (plate 12c). The burrow is preserved as an endichnion within a hard, non-fissile, purple shale. It is surrounded by two concentrically arranged halos, an inner 2 mm thick, pale green halo, and an outer 1.5 mm thick, black halo (plate 12a).

Discussion

Strictly speaking, this form conforms to the diagnosis of *Planolites* and not that of *Palaeophycus*. It is impossible however, to reconcile a quartzite infilled burrow, within a monolithic shale, as having been made by a sediment ingesting, active back-filling behaviour as is ascribed to *Planolites* (Pemberton and Frey, 1982). There is no indication that these burrows were part of a *Chondrites*-like system. Thus, this form must represent a simple, open burrow emplaced within muds and passively infilled by sand. Such a burrow would be constructively and ethologically identical to the interpretation of *Palaeophycus*, except for the lack of a distinct lining. However, in a firm and cohesive mud, a thick lining would not be necessary to maintain an open burrow. These burrows probably had a thin mucus lining and, as is proposed for *Chondrites*, this is not visibly preserved in the resulting trace fossil (see Ichnogenus *Chondrites* and Ichnogenus *Skolithos*). These burrows are assigned to ?*Palaeophycus* since they are morphologically and ethologically similar to specimens of *P. tubularis*, except that no lining is apparent. They are also similar to *Trichophycus* but lack the wall ornamentation that would be expected in an arthropod trace emplaced in cohesive mud.

The unusual annulated specimen was undoubtedly an open burrow, however, it is not possible from the small fragment recovered to tell if it was a domicile or the burrow of a motile trace maker. The fine annulations suggest peristaltic contractions were used to move the trace maker within the burrow. The colour banding must be the result of pore water permeating through the porous burrow infill and affecting the diagenesis of the surrounding mud.

Ichnogenus *Phycodes* Richter, 1850

Type Ichnospecies

Phycodes circinatum Richter, 1853, by subsequent designation of Mägdefrau, 1934

Diagnosis

Systems of acutely branching, unlined, horizontal burrows with retrusive spreiten. These may form flabellate or broom-like bundles or longer linear structures that range from straight to circular. Branches commonly curve upwards and may be covered with fine annulae or striae. (adapted from Osgood, 1970; Crimes and Anderson, 1985)

Stratigraphic Range

Phycodes has been reported from rocks of Early Cambrian to Miocene age (Häntzschel, 1975).

Discussion

Phycodes is one of the most confusing ichnogenera with respect to the range of morphotypes it includes. Its original diagnosis consists of a short main shaft that curves down to horizontal and gives rise to a number of short, acutely branching, upward curving burrows with retrusive spreiten (Osgood, 1970). The general form is a broom-like or palmate bundle of burrows (Osgood, 1970). There are two newer forms however, *Phycodes pedum* Seilacher, 1955, resembling a crude feather-stitch pattern, and *Phycodes coronatum* Crimes and Anderson, 1985, a horizontal, circular main shaft which gives rise to branches, with retrusive spreiten, off the outer circumference of the main burrow. These two forms are much more linear compared to the compact, bundled forms classified in the late eighteen-hundreds (see Osgood, 1970; Crimes and Anderson, 1985).

Thus, the primary diagnostic feature of *Phycodes* must be a system of branching burrows with retrusive spreiten (Osgood, 1970). The pattern of branching is used to separate out the different ichnospecies (see Osgood, 1970 for a detailed discussion of the ichnotaxonomy of *Phycodes*). It is uncertain as to whether the different ichnospecies of *Phycodes* have any environmental or ethological significance or whether they simply reflect different types of trace makers with different inherited behaviour patterns. Some examples of *Phycodes* are transitional with *Chondrites* (Chamberlain, 1977), however, *Phycodes* can be distinguished by its tighter, more acute branching; spreiten; and close vertical stacking of burrows (Osgood, 1970).

Phycodes is found on the lower bedding surfaces of thin, fine sandstones and siltstones that overlie shale (Osgood, 1970). The proximal main shaft curves down into the shale and the branches curve back into the overlying sandstone or siltstone. Distal connections to the sediment surface can sometimes be discerned (Osgood, 1970).

Phycodes represents the deposit-feeding activities of small animals mining localised patches of organic rich sediment trapped along sand/mud interfaces (Seilacher, 1955; Eagar *et al.*, 1985). Retrusive spreiten are produced as a result of the trace maker pulling material off the ceiling and packing it, along with fecal material, onto the floor of the burrow (Osgood, 1970). Thus, *Phycodes* burrows and spreiten are usually sand infilled. It is uncertain whether the compactness of this ichnogenus is a direct response to patchily distributed organic matter or a behavioural artifact of the particular habits of the trace makers. *Phycodes* is indicative of low energy conditions with an abundant supply of organic material settling onto the bottom and periodic high energy events that deposit sand sized material, burying the organics. Unlike *Chondrites*, however, *Phycodes* is generally formed close to the sediment surface, and is most commonly associated with thinly-bedded deposits (Osgood, 1970). Like *Chondrites*, this behaviour may enable the trace maker to utilise dysoxic, organic rich zones, at sand/mud interfaces, since the trace maker works from an open burrow within overlying oxygenated coarse silts and sands (Jordan, 1985). All the *Phycodes* in this study are preserved on or near the base of thin to moderate quartzite beds.

Phycodes is commonly associated with shallow marine to intertidal, moderately thick energy environments with fine to moderate interbedding of sand and mud (Seilacher, 1964; Baldwin, 1977a; Crimes *et al.*, 1977; Crimes and Anderson, 1985; Legg, 1985). However, it ranges into both deep sea environments (Chamberlain, 1977) and brackish water settings (Pollard, 1981). *Phycodes* is usually attributed to vermiform organisms (Osgood, 1970; Häntzschel, 1975; Chamberlain, 1977; Crimes *et al.*, 1977) although small animals from almost any phylum could be responsible (Osgood, 1970).

Phycodes circinatum Richter, 1853
plate 14c, d

Diagnosis

Bundles of thin, cylindrical, unlined tubes that branch out from a common point at acute angles. Proximal sections are close packed with retrusive spreiten. Distal sections are thinner and distinctly separate. Branches are usually finely annulated. (after Crimes, 1969; Osgood, 1970)

Occurrence

Phycodes circinatum was found in subunits 2b, 2e, 2o, 5b, 5d, 6a, and 6g, and on float at Lake O'Hara.

Description

Specimens consist of tightly packed, conical to broom shaped bundles of 1–2 mm diameter, unlined, quartzite infilled tubes. The bundles inscribe angles of approximately 10°. Tube thickness increases slightly towards the narrower end of the bundle. Vague spreite can sometimes seen in transverse section from the narrow, proximal end to approximately the midsection of the bundles. Whether these are protrusive or retrusive spreite can not be determined due to the tight packing of the tubes. The longest exposed length of a bundle is 20 mm. Specimens are preserved as hypichnia on thin quartzite beds, within dark coloured shales.

Discussion

Phycodes circinatum is distinguished from other bundle shaped *Phycodes* by its fine burrows, averaging 1.3 mm in diameter; the large number of branches; and the fine annulations (Osgood, 1970). The specimens in this study are diagnosed on the basis of the large number of fine burrows seen in transverse section. *Phycodes circinatum* has previously been reported only from the Lower Ordovician (Crimes, 1987).

Phycodes flabellum (Miller and Dyer, 1878)
plate 13a

Diagnosis

Bundles of close spaced burrows arranged in a tight fan-shaped pattern. Individual burrows are cylindrical and annulate with no vertical spreite. (after Osgood, 1970)

Occurrence

Phycodes flabellum was found in subunits ?4h, 4m, 4n, 4o, 4r, and 4x, and on float at Lake O'Hara.

Description

Specimens consist of dense, broom-like fans of 3–8 mm diameter, unlined, quartzite infilled tubes. These tubes overlap laterally and vertically along their entire length, often giving the impression of a bundle of scratch marks. Bundles are up to 100 mm long, inscribing angles of 10–30° and are straight to gently curved along length. Specimens are preserved as hypichnia on thin quartzite beds within dark coloured shales.

Discussion

The specimens in this study are similar in form and construction to *Phycodes flabellum* described by Osgood (1970, plate 65, figure 1) except that there are no visible annular rings on the branches.

Phycodes ?flabellum (Miller and Dyer, 1878)
plate 14e

Occurrence

Phycodes ?flabellum was found in subunit 6a and on float in unit 3.

Description

Specimens consist of 50–120 mm diameter rings made up of 5–50 mm wide burrows with prominent lateral spreiten. Burrow width varies by as much 35 mm within specimens, resulting from expanded lateral spreiten. There are occasional straight, tangential extensions, approximately the same width as the narrowest portion of the ring. Specimens are preserved as hypichnia on thin quartzite beds within dark coloured shales.

Discussion

These specimens are similar in construction to samples of *Phycodes flabellum* except that the fan of burrows circles back on itself. The extensions off the main ring of spreiten may represent the main shaft of the burrow system. The circular form is similar to *Phycodes coronatum*, however, *P. coronatum* does not possess lateral spreiten in its main ring (Crimes and Anderson, 1985). The circular form of these specimens may reflect the optimal utilisation of particularly localised, organic rich deposits.

Phycodes palmatum (Hall, 1852)
plate 13c, d, e

=*Buthrotrephis palmata* Hall, 1852 (Osgood, 1970)

Diagnosis

Phycodes consisting of a small number of thick, acute branches, with poorly developed retrusive spreiten (after Crimes *et al.*, 1977).

Occurrence

Phycodes palmatum form A is found in subunits 2j, 2l, 2o, 2s, 4m, 4o, and possibly in 5b, 5d, and 6a. *P. palmatum* form B is found in subunits 2b, 4h, 4m, 4o, 4r, 4s, 4t, 4x, 5d, 6a, 6e, and 6g.

Description

Specimens of *Phycodes palmatum* form A consist of 1–10 mm wide, unlined, quartzite infilled burrows with lengths approximately 5 times the burrow diameter (plate 13c, d). The burrows taper to a narrow point at one end and are blunt and rounded at the other. The blunt ends of the burrows are usually covered by spreiten-like transverse striations. The entire structure consists of 2–3 such burrows, joined at the narrow end. Specimens were preserved as hypichnia on thin quartzites within dark coloured shales.

Specimens of *Phycodes palmatum* form B consist of 5–15 mm long, 3–5 mm diameter, unlined, quartzite infilled tubes that give rise to numerous branches, of similar structure and size, at one end and taper off at the other end (plate 13e). Branches are separated by 0–2 mm and have vague spreite in some cases. These structures frequently form broad arcs with the branches occurring predominantly along the inside of the arc. Specimens are preserved as hypichnia on thin quartzites within dark coloured shales.

Discussion

Both of these forms had few, poorly developed retrusive spreiten at the middle to distal ends of the branches. They conform to Osgood's (1970) description of *Phycodes palmatum* as a small number of distinct, well spaced probings that terminate or curve upward abruptly. Form A appears to represent repeated broadly concave up probings along roughly the same horizontal plane. Form B is similar to *Phycodes circinatum* in that it consists of a more three dimensional bundle, however, there are fewer branches and these are much larger and more distinctly spaced. The overall branching pattern is shorter and more compact than *Chondrites* form D from this study.

Some authors (see Osgood, 1970) question whether *Buthrotrephis palmata* should be assigned to *Phycodes* as the branching pattern is similar to *Chondrites* and the evidence for spreite is vague in most specimens. Although the overall form of the specimens in this study is very similar to *Chondrites*, one or more poorly developed retrusive spreiten were visible on the branches of most specimens. As well, at least some specimens of *Buthrotrephis palmatum* in the literature (Seilacher, 1955) show evidence of retrusive spreiten. Thus the the author agrees with others (Seilacher, 1955; Crimes *et al.*, 1977) that, at least until a thorough review of the ichnospecies is carried out, *Buthrotrephis palmatum* should be synonymised with *Phycodes palmatum*.

Ichnogenus *Planolites* Nicholson, 1873

Type Ichnospecies

Planolites vulgaris Nicholson and Hinde, 1875, (=*Planolites beverleyensis* (Billings, 1862)) by subsequent designation of Alpert, 1975

Diagnosis

Unlined, rarely branched, straight to tortuous, smooth to irregularly walled or annulate burrows, circular to elliptical in cross-section and of irregular dimensions and configurations. The infilling is essentially structureless, differing in lithology from the host rock. (Pemberton and Frey, 1982)

Stratigraphic Range

Planolites ranges from the Precambrian to the Recent (Häntzschel, 1975).

Discussion

Planolites consists of unlined cylindrical to subcylindrical burrows. The infill is structureless to vaguely backfilled and is lithologically distinct from the host rock, usually of a slightly coarser grain size. There can be a range in burrow dimensions both between and within specimens in a sample. Burrows vary from straight to highly tortuous, and become more tortuous with more frequent overcrossing and interpenetration as burrow density increases. (Pemberton and Frey, 1982)

Planolites is interpreted to be the actively backfilled burrow of motile, vermiform deposit-feeders (Pemberton and Frey, 1982). The differences between the infill and host rock arise from processing of the sediment either before ingestion or during digestion. (Pemberton and Frey, 1982).

Planolites has a eurybathic distribution (Crimes, 1970b) and is indicative of brackish to near normal salinity (Pienkowski, 1985; S.G. Pemberton, pers. comm., 1988), soft to soupy substrates (Ekdale *et al.*, 1984), and well oxygenated conditions within the sediment (Bromley and Ekdale, 1984) since no free connection with the water column is maintained during its production. The simple structure and extensive geologic time range of *Planolites* suggests that a large number of different biotaxa are responsible for its production (Pemberton and Fey, 1982; Crimes and Anderson, 1985).

Planolites in this study is most common in thinly interlaminated sandstone and shale and on the basal bedding surfaces of thicker quartzites. The burrow infill is usually a relatively clean quartzite however, similar to ?*Palaeophycus*. This can be explained by the fact that the volumetric proportion of shale in the host rock is quite small although it is conspicuous by the fact that it is concentrated in thin layers. When this sediment is homogenised in the *Planolites* infill, the mud fraction becomes much less conspicuous and the infill takes on the appearance of a clean quartzite.

Planolites annularis Walcott, 1890
plate 9e

Diagnosis

Distinctly annulate, subcylindrical burrows (Pemberton and Frey, 1982).

Occurrence

Planolites annularis was found in subunits 2b, 2j, 2v, 4m, 4w, 5d, 6a, and 6c, as well as on float at Moraine Lake and Lake O'Hara.

Description

Specimens consist of straight to gently curving, unlined, 3–6 mm diameter burrows with regular, 1 mm wide, 1–2 mm spaced, smooth but distinct annular rings. Burrows are horizontal to slightly inclined with respect to bedding. Burrow diameter is constant along length, aside from the annulations. The burrows are preserved as endichnia and convex epichnia and hypichnia within a wide range of rock types from shale to silty quartzite. The infill is always a coarse quartzite. *Planolites annularis* burrows occur as isolated structures, either alone or within sparsely bioturbated samples.

Discussion

The annulations ornamenting this ichnospecies reflect a mode of propulsion that utilised peristaltic contractions, similar to the strategy used by earthworms (Frey and Pemberton, 1982).

Planolites beverleyensis (Billings, 1862)
plate 9f

Diagnosis

Relatively large, smooth, straight to gently curving or undulose, cylindrical burrows

(Pemberton and Frey, 1982).

Occurrence

Planolites beverleyensis is found in subunits 2a, 2j, 2l, 4o, 4r, 6a, and 6c, as well as on float at Moraine Lake and Lake O'Hara.

Description

Specimens consist of straight to curving, unlined, smooth walled, horizontal to slightly inclined burrows. Burrow diameter varies from 6–14 mm and is constant along the length of a burrow. Specimens are preserved as endichnia and convex epichnia and hypichnia within a wide range of rock types, usually thinly interbedded shale and quartzite or gritty shale. The infill is usually a coarse, dirty quartzite, except were the trace fossil occurs in gritty mudstones. In this case, the infill is a more sand rich mudstone than the surrounding rock.

Specimens of *Planolites beverleyensis* are most commonly found as dense, overcrossing, assemblages without other burrow types, although they are occasionally found as isolated burrows within moderate to well bioturbated samples. Assemblages of *Planolites beverleyensis* often vary considerably in diameter from one burrow to another. Due to the density of burrows however, it is difficult to tell whether or not this is a real difference or caused by exposure at different levels within the sample.

Planolites montanus Richter, 1937

plate 9d

Diagnosis

Relatively small, curved to contorted burrows (Pemberton and Frey, 1982).

Occurrence

Planolites montanus is found through out units 2 and 4, and in subunits 3b, 3f, 5b, 5d, 5h, 6a, 6c, and 6d, as well as on float at Moraine Lake and Lake O'Hara.

Description

Specimens consist of straight to tortuous, unlined, smooth walled, horizontal to near vertical burrows. Burrow diameter varies from 2–6 mm and is constant along the length of a burrow. The burrows within a single sample are usually within 2 mm in diameter of each other. Where this is not the case, there are usually two or more distinct size classes present. Specimens are preserved as endichnia and convex epichnia and hypichnia within a wide range of rock types, usually thinly interbedded shale and quartzite or gritty shale. The infill is usually a coarse, dirty quartzite.

Planolites montanus is commonly found as dense, overcrossing, intertwining, monotaxonomic assemblages occupying horizons a few centimetres thick. It is also found as isolated burrows within ichnotaxonomically diverse, moderate to well bioturbated samples. These occurrences are generally less tortuous.

Discussion

Planolites montanus and *P. beverleyensis* are often found together, and in such cases comprised easily distinguished size classes. When they were found apart however, the diameter range of the two ichnospecies could be seen to overlap by approximately 2 mm over all occurrences in the study. Thus, ichnotaxonomic assignments may not be accurate in marginal specimens. The primary difference between these two ichnotaxa is burrow diameter (Pemberton and Frey, 1982), thus, these two ichnospecies probably reflect a taxonomic difference in the respective trace makers. Where distinct size classes of *Planolites montanus* occur together, they probably reflect the presence of more than one type of infaunal trace maker.

The density of burrows is probably directly proportional to the abundance of organic detritus within the sediment. The increase in burrow tortuosity with density indicates that the trace makers avoided interpenetrating previous burrows where possible.

Ichnogenus *Protichnites* Owen, 1852

?=*Angulichnus* Elliott and Martin, 1987
?=*Asaphoidichnus* Miller, 1880 (*Partim*) (*in* Osgood, 1970)
?=*Kouphichnium* Nopcs, 1923 (*in* Häntzschel, 1975)
?=*Maculichna* Anderson, 1975 (*in* Archer and Maples, 1984)
?=*Mesichnium* Gilmore, 1926 (*in* Häntzschel, 1975)
?=*Merostomichnites* Packard and Caster, 1938 (*in* Osgood and Drennen, 1975)
?=*Octopodichnus* Gilmore, 1927 (*in* Häntzschel, 1975)
?=*Oniscoidichnus* Brady, 1949 (*in* Häntzschel, 1975)
?=*Palmichnium* Richter, 1954 (*in* Häntzschel, 1975)
?=*Permichnium* Guthorl, 1934 (*in* Häntzschel, 1975)
?=*Petalichnus* Miller, 1880 (*in* Häntzschel, 1975)
?=*Pterichnus* Hitchcock, 1865 (*in* Archer and Maples, 1984)

?=*Tasmanadia* Chapman, 1929 (*in* Häntzschel, 1975)
?=*Teratichnus* Miller, 1880 (*in* Osgood, 1970)
?=*Trachomatichnus* Miller, 1880 (*Partim*) (Osgood and Drennen, 1975)
?=*Triavestigia* Gilmore, 1929 (*in* Häntzschel, 1975)
?=*Umfolozia* Savage, 1971 (*in* Häntzschel, 1975)

Type Ichnospecies

Protichnites septemnotatus Häntzschel, 1962

Diagnosis (Emended)

Trackways made up of two parallel rows of imprints separated by a median zone. Medial or lateral ridges may be present. The two rows of imprints may be broken up into serially repeated shorter rows that are oblique to the overall trend of the track. (emended from Osgood, 1970; Häntzschel, 1975; Osgood and Drennen, 1975; Bromley and Asgaard, 1979). The original diagnosis is similar except the presence of median ridges is diagnostic (Häntzschel, 1975).

Stratigraphic Range

Protichnites, as defined by Häntzschel, ranges from the Cambrian to the Ordovician (Häntzschel, 1975). The ichnogenus, as emended above, may have a substantially greater stratigraphic range.

Discussion

Protichnites, as it is currently defined, consists of two parallel rows of serially arranged imprints with a median gap containing continuous or intermittent ridges (Häntzschel, 1975). It is interpreted as the walking trace of a trilobite or similar animal (Osgood and Drennen, 1975). The imprints are impressions of the ends of the appendages and the medial ridges are interpreted to be drag marks of posterior structures, such as pygidia or caudal cerci (Osgood and Drennen, 1975).

Arthropod surface locomotion traces are indicative of hydrodynamic conditions calm enough to permit the animals to remain exposed up off the sediment surface without being swept away during the period of time that the trace is made (Crimes, 1970c). Any preferred association with long term quiet water environments may simply be a result of the low preservation potential of such traces in settings experiencing even minimal erosion. Most arthropod surface trackways have only been found in fully marine deposits to date (Osgood and Drennen, 1975).

Protichnites is currently diagnosed as being a paired, serial trackway of bifid or trifid imprints with a continuous to intermittent, single or paired medial groove (Häntzschel, 1975; Osgood and Drennen, 1975). This diagnosis differs from all the members of the proposed synonymies list only in the exact morphology of the imprints and the presence of medial ridges. These differences have been utilised in the ichnotaxonomy of the traces as they are thought to give an indication of the taxonomy of the trace maker. However, as discussed under *Cruziana*, *Diplichnites*, and *Monomorphichnus*, such details are actually unreliable indicators of trace maker anatomy. Moreover, the biotaxonomic significance of these features is poorly understood at best. Thus, ichnogeneric distinctions based on imprint patterns can only have a very low level of significance. As well, dividing up all these forms masks a profound ethological characteristic that they all share. *Protichnites* in the sense it is used in the emended diagnosis, including all those forms in the proposed synonymy, corresponds to locomotion produced by applying force from an appendage held stationary with respect to the substrate. This produces two rows of blunt impressions in a bilaterally symmetrical trace maker, along with what ever drag marks are produced by stationary body parts in contact with the sediment. Movement in which the body axis is oblique to the direction of motion would result in a series of oblique rows of imprints with the number of imprints in each row corresponding to the number of appendages used by the trace maker, not necessarily the number of appendages that the trace maker possessed (Osgood, 1970). (see discussion of *Diplichnites* for the relationship of the emended *Protichnites* to other arthropod surface tracks)

All the trace fossils in the synonymy list, including *Protichnites*, have been interpreted as the walking traces of arthropod-like animals and cephalopods (Osgood, 1970; Häntzschel, 1975; Archer and Maples, 1984). However, brittle stars, sea urchins, and morid fish make similar traces and some holothurians make tracks very similar to *Petalichnus* or *Trachomatichnus* (Heezen and Hollister, 1971).

The emended *Protichnites* would be indicative of at least periodic quiet water conditions in a marine environment. It would have a eurybathic distribution from abyssal trenches to intertidal flats (Heezen and Hollister, 1971; Osgood and Drennen, 1975). Its stratigraphic range would likely be from the late Precambrian to the Recent.

Protichnites ichnosp.
plate 10a, e

Occurrence

Protichnites ichnosp. is most common on float at Moraine Lake, with single occurrences of the simplest forms in subunit 6e and at Lake O'Hara.

Description

Trackways consisting of two parallel rows of protuberances separated by a wide, featureless median groove. There are three varieties: those with simple, roughly circular protuberances; those with elongate protuberances with the long axis roughly perpendicular to the trend of the track (plate 10e); and those with compound protuberances composed of distal, elongate protuberances, perpendicular to the track trend and proximal, circular protuberances (plate 10a). The elongate protuberances are striated transversely to their long axis. The last two varieties are found only at Moraine Lake.

Discussion

All three forms result from an animal walking across the sediment surface. The first variety is similar to the present diagnosis of *Protichnites* except that there are no medial drag marks. The second is similar to *Permichnium* and *Tasmanadia* which have long, thin, paired imprints. The third variety, with compound imprints, is similar to either *Merostomichnites* or *Umfolozia*. The brush-like outer impressions suggest that the trace maker had compound appendages with an outer element similar to the comb-like exites of many trilobites (see Whittington, 1980). Assuming that it was made by a trilobite, it indicates that the exite branch of at least some trilobites could easily be brought into contact with the sediment along with the telopodite branch of the same appendage, and with sufficient force to cause a strong imprint. This corresponds to an appendage construction similar to Bergström's (1972) reconstruction of *Cryptolithus*, in which the exite fringe hangs down outside the telopodite.

?*Protichnites*

plate 17d

Occurrence

?*Protichnites* is found in subunit 6e.

Description

Specimens consist of 3 mm wide trackways composed of two parallel rows of 1.5 mm long imprints oriented perpendicular to the trend of the track.

Discussion

This form of *Protichnites* is similar to *Trachomatichnus*, *Diplichnites triassicus* Link, 1943 (Bromley and Asgaard, 1979, figure 16f), and ?holothurian tracks from deep ocean trenches (Heezen and Hollister, 1971, figure 3.12). It is difficult to imagine an arthropod trace maker, only 3 mm wide walking on 1.5 mm wide appendage surfaces. Thus, since the Gog Group is older than the oldest occurrence of holothurians (Boardman *et al.*, 1987), these trace fossils may correspond more closely to a *Diplichnites* behaviour.

Ichnogenus *Protopaleodictyon* Ksiazkiewicz, 1970

=*Protopalaeodictyon* Ksiazkiewicz, 1958 (*nomen nudum*, Seilacher, 1977b)

Type Ichnospecies

Protopaleodictyon incompositum Ksiazkiewicz, 1970

Diagnosis

Uniramous and biramous graphoglyptid burrows consisting of wide first order meanders and sine wave shaped second order undulations with distinct appendages [*sic*], all at the same level (Seilacher, 1977b).

Stratigraphic Range

Protopaleodictyon has been reported from the Lower Cambrian to the Tertiary (Häntzschel, 1975; Crimes and Anderson, 1984).

Discussion

Protopaleodictyon consists of a fine burrows inscribing first and second order meanders with small branches off the corners of the smaller order meanders (Seilacher, 1977b). They are post depositional structures formed on the lower bedding surfaces of thin, fine sandstones (Ksiazkiewicz, 1977). The burrows are irregularly infilled and left partially open (Ksiazkiewicz, 1977). Collapse structures can sometimes be seen (Ksiazkiewicz, 1977).

These graphoglyptids are interpreted to be the result of organised deposit-feeding (Ksiazkiewicz, 1977). Although they are commonly associated with deep water flysch deposits (Ksiazkiewicz, 1977), Lower Cambrian examples are sometimes found in near shore marine settings (Crimes, 1974; Crimes and Anderson, 1985). Crimes and Anderson (1985) found similar occurrences of organised feeding behaviours (such as *Paleodictyon* Meneghini *in* Murchison, 1850) in Lower Cambrian shallow marine settings. This is interpreted as indicating that the complex deposit-feeding and farming behaviours, common in deep sea settings later in the Phanerozoic, actually evolved in shallow water in the early Cambrian and moved into the deep sea as a result of ecological pressure (Crimes, 1974; Crimes and Anderson, 1985).

Seilacher (1977b) suggested that *Protopaleodictyon* branches could anastomose to form *Paleodictyon*-like nets, although no such transition has actually been documented. The genetic relationship between *Protopaleodictyon* and *Paleodictyon* is unclear however, since the former is a partially backfilled deposit-feeding trace and the latter is a maintained, open burrow system.

Protopaleodictyon ichnosp.

plate 10b

Occurrence

A single specimen of *Protopaleodictyon* was found in subunit 6c.

Description

An irregularly meandering 1 mm wide burrow preserved as concave hypichnia on a 5–10 mm thick quartzite lentil within silty, beige coloured shale. The meanders are composed of 2–10 mm long, relatively straight segments separated by smooth turns varying from 10–90°. There are 1–10 mm long branches extending from each turn at irregular angles. In some cases, these branches fork within 1–5 mm of their end. Some branches appear to join together to form irregularly shaped polygons. The specimen was less than 50 square centimetres so that the presence of larger orders of meanders could not be verified.

Discussion

This structure is similar to the description of *Protopaleodictyon submontanum* Azpeitia, 1933 (Ksiazkiewicz, 1977) in that the small order meanders are irregular. The instances in which branches from different meanders appear to join together probably do not indicate a transition between this ichnogenus and *Paleodictyon*, rather they are probably chance events resulting from the high burrow density.

Ichnogenus *Rusophycus* Hall, 1852

=*Isopodichnus* Bornemann, 1889 (Bromley and Asgaard, 1979)

Type Ichnospecies

Fucoides biloba Vanuxem, 1842, by subsequent designation of Seilacher, 1955

Diagnosis

Two short lobes separated by a median gap or groove. Outer lobes and marginal ridges may be present. The lobes may be parallel or divergent and vary from smooth to covered with transverse to longitudinal, scratch-like striations. The dimensions of the lobes and nature of the scratch marks may vary along length. The striations can be single or bundled. The median gap can be featureless or show segmentation. (after Osgood, 1970; Häntzschel, 1975).

Stratigraphic Range

Rusophycus is known to range from the Lower Cambrian to the Jurassic (Crimes, 1970b; Häntzschel, 1975; Bromley and Asgaard, 1979; Pienkowski, 1985).

Discussion

General Description

Rusophycus consists of two short lobes separated by a median groove or gap (Crimes, 1970c; Osgood, 1970; Seilacher, 1970). It is similar in form to *Cruziana* except that rather than forming long furrows, *Rusophycus* forms short, buckle-shaped structures. The lobes are generally covered with transverse to oblique scratch marks. Like *Cruziana*, *Rusophycus* is almost always preserved as a positive relief cast on the base of sandstone and siltstone beds overlying siltstone or shale (Crimes, 1970c; Osgood, 1970; Seilacher, 1970; Goldring, 1985).

A survey of the literature shows that *Rusophycus* exhibits an extremely wide range in morphology (Fenton and Fenton, 1937; Crimes, 1970b; Osgood, 1970; Seilacher, 1970, 1985; Bergström, 1976; Crimes *et al.*, 1977). The relief (depth) varies from extremely shallow structures, transitional with *Diplichnites*, to steep-sided pits with depth to width ratios greater than 1. The lobes may slope down and/or taper toward one or both ends. In extreme cases, the trace fossil may consist of a steep wall at one end and slope back level with bedding at the other. The median line varies from a groove to a distinct gap and can be of constant width, gape towards one or both ends, or narrow at both ends. Gaps are usually featureless, however, in some forms they are made up of a double row of smooth, flat topped, rectangular mounds. The margins and sides of *Rusophycus* specimens often exhibit one or more ridges which can be continuous or segmented and enclose a variable proportion of the circumference of the trace fossil.

The range in scratch mark patterns in *Rusophycus* is almost identical to that of *Cruziana*. A small number of forms have a double lobe structure, similar to *Cruziana arizonensis* or *C. semiplicata*, with medial lobes covered by coarse, near transverse scratch marks and lateral lobes covered by finer, more longitudinal scratch marks (Seilacher, 1970; 1985, Bergström, 1973). The lateral lobes of *Rusophycus* are generally most prominent towards the back end (Bergström, 1973; Seilacher, 1985). The boundary between medial and lateral lobes may be marked by no more than a subtle shift in scratch mark pattern (Bergström, 1973). *Rusophycus* can occur as both isolated structures and components of *Cruziana* and *Diplichnites* trackways (Crimes, 1970c; Seilacher, 1970, 1985; Osgood and Drennen, 1975; Bergström, 1976; Baldwin, 1977a).

Interpretation

The history of *Rusophycus* mirrors that of *Cruziana* in that it was originally interpreted to be the remains of plant material (Osgood, 1970; see Osgood, 1970 and Häntzschel, 1975 for a thorough review of the history of *Rusophycus*).

The currently accepted interpretation is that *Rusophycus* are the remains of actively excavated pits. These were either emplaced as open structures at the sediment water interface, and infilled some time after formation (Crimes, 1975b; Baldwin, 1977a; figure 9), or as part of more complex intrastratal structures, either true burrows or temporary structures that collapsed after passage of the trace maker (Goldring, 1985; Seilacher, 1985; see Ichnogenus *Cruziana*, Emplacement and Preservation). *Rusophycus* differs from *Cruziana* in that *Rusophycus* involves little or no forward movement of the trace maker during production or inhabitation of the trace (Crimes, 1970c, 1975b; Seilacher, 1985).

While no modern analogues of *Cruziana* making activities are known (Whittington, 1980); modern phyllopods have been observed making *Rusophycus* on the sediment surface in brine pools and limulids produce similar intrastratal traces (Osgood, 1970).

Trace Makers

Most early to mid Paleozoic examples of *Rusophycus* are presumed to have been made by trilobites. As would be expected, direct evidence for the identity of the trace makers for *Rusophycus* is rare (see Ichnogenus *Cruziana*). Some notable examples exist, however, where the trace maker is preserved in the trace fossil. Orlowski *et al.* (1970, plate 3.a) figured an *Olenus rarus* embedded in the sediment in a position that is consistent with *Rusophycus*, and in a horizon with abundant *Rusophycus rusoformis* Orlowski *et al.*, 1970 of similar dimensions. Osgood (1970) figured specimens of *Rusophycus pudicum* Hall, 1872 with *Flexicalymene meeki*, a trilobite, preserved in the burrows. Zell (1988) figured a *Phacops rana* in a *Rusophycus*-like burrow. In this case, the deep burrow form and tail down position of the trilobite are similar to *Rusophycus leifeirikssoni* Bergström, 1976 or *Rusophycus navicella* Fenton and Fenton, 1937. These examples are understandably rare as a trilobite would either have to die of "natural causes" in its burrow and be buried before decomposing or be buried so quickly and deeply that it could not even attempt to dig itself out.

There is a wealth of indirect evidence indicating a trilobite origin for most *Rusophycus*. Trilobites and *Rusophycus* have stratigraphic ranges which mirror each other with respect to abundance, diversity, average size, and maximum size (Bergström, 1973; Ekdale *et al.*, 1984; Seilacher, 1985). The oval outline of *Rusophycus* matches that of trilobites but is dissimilar to most other arthropods (Bergström, 1973). Impressions of other anatomical features are indicative of a trilobite origin, including impressions of genal spines, pleurae, arrangement of the coxae, and the overall shape (Osgood, 1970; Seilacher, 1970, 1985; Bergström, 1973; Osgood and Drennen; 1975). These are sometimes diagnostic enough to identify the particular trace maker (Bergström, 1973; Crimes, 1975a; Osgood and Drennen, 1975). As well, the typical scratch mark pattern of *Rusophycus* is indicative of serially arranged, undifferentiated appendages, consistent with the morphology of trilobites as well as some other arthropod groups (Bergström, 1973).

Several forms of *Rusophycus* are known to have been produced by non-trilobite arthropods, including limulids (Seilacher, 1985) and branchiopods (Trewin, 1976; Seilacher, 1985). The diagnostic features are imprints of prosomal margins and position of scratch marks in the former, and the small size and environmental setting in the latter. The production of *Rusophycus* has been observed by phyllopods and limulids in the modern (Osgood, 1970).

Mechanics of Formation

The mechanics of formation of *Rusophycus* are the same as those of *Cruziana* except that the medial and postero-medial digging strokes only excavated sediment and did not generate any propulsive forces. The reasoning and evidence for attributing the coarse scratch marks to the telopodites is the same as that used for *Cruziana* (see Ichnogenus *Cruziana*, Mechanics of Formation). Marginal ridges are attributed to impressions of the genal spines (Crimes, 1970c, 1975a, 1975b; Seilacher, 1970) and the pleurae (Seilacher, 1970). Segmented marginal ridges are produced by the pleurae (Seilacher, 1970). These features differ from comparable ones in *Cruziana* in that the shape of the marginal ridges reflects the actual shape of the skeletal feature that made them, rather than its cross-sectional shape perpendicular to motion, as for *Cruziana*.

The forward direction in *Rusophycus* can be independently determined in those specimens that preserve impressions of the cephalon and genal spines. These cases, as well as specimens with the trace maker preserved *in situ*, have shown that scratch marks usually become finer towards the posterior of the trace (Seilacher, 1985) and, that where the median gap widens in one direction, this end is usually the front (Crimes, 1975b).

The contention that the direction of motion of the appendages was medially to postero-medially directed in trilobite produced *Rusophycus* (Osgood, 1970; Seilacher, 1970, 1985) is supported by several lines of evidence. Sediment piles are never found along the sides of the traces (Seilacher, 1985) although these might easily have been washed away. Where forward direction can be determined, oblique scratch marks always form anterior opening V-marks (Seilacher, 1970, 1985). Functional morphological analyses of trilobite appendages confirms that a postero-medial directed digging stroke is the most likely (Whittington, 1980). However, appendage motion is not postero-medially directed in all cases, especially in non-trilobite produced forms of *Rusophycus* (Osgood, 70; Bergström, 73; Seilacher, 1985). *Limulus* for example, pushes sediment back and out rather than back and in (Osgood, 1970; Seilacher, 1985).

Cross-cutting relationships between *Rusophycus* scratch marks (Häntzschel, 1975) can be used to determine that the serial waves of appendage motions progressed from back to front in trilobites, as was proposed by Seilacher (1955). Scratch marks in *Rusophycus* often trend from near transverse at the front end to strongly oblique near the back end. Seilacher (1985) noted a progressive, front-to-back decrease in the strength of scratch mark impression in many *Rusophycus*. These features suggest that the anterior appendages concentrated on digging and the rear appendages concentrated on pushing sediment back out of the burrow. This explains why deep *Rusophycus* are usually deeper towards the front end.

The cephalon may have been used to assist the production of *Rusophycus*, by scooping out a short furrow as an initial excavation; by continuous shovelling; or by levering the front of the trace maker into the sediment at the start of the excavation, thereby pushing the strong anterior digging legs into the sediment. This latter process is used in the burrowing process of *Limulus* (see Eldredge, 1970). The curved prosoma (front margin) of *Limulus* appears to be adapted to this purpose (Eldredge, 1970). Several authors have noted a similarity in the curvature of the anterior margin of the cephalon in some trilobites that could have been adapted to this function (Eldredge, 1970; Bergström, 1972; Speyer, 1988; figure 6). In some forms of *Rusophycus* (see *R. jenningsi*) the cephalon shovelled sediment throughout the burrowing process as shown by numerous horizontal ridges along the front face of the trace fossil.

Lateral lobes are found in a small number of ichnospecies of *Rusophycus* (Seilacher, 1970). They are usually covered with fine, near longitudinal lineations or fine, oblique to longitudinal scratch marks (Seilacher, 1970). These are assumed, in most cases, to have been produced by the exites (Seilacher, 1970; Bergström, 1973). Lateral lobes are usually found towards the back of *Rusophycus*, indicating that it was usually the rear exite branches that were designed to manipulate sediment (Bergström, 1973; Seilacher, 1985). The function of the exite branches was either to assist in digging (Bergström, 1976) or to help push sediment out the back of the trace maker by generating backward directed currents (Whittington and Almond, 1987; figure 11). Digging and excavation may have alternated a number of times in the generation of most *Rusophycus*, especially in deposit-feeding forms of this activity. Sediment could have been dug up, pushed to the coxae, and sorted through for food then the loose sediment pushed out, by either the telopodites or exites.

The smooth, square impressions in the median gaps of some *Rusophycus* are interpreted to have resulted from the motion of the coxae (Seilacher, 1970; Bergström, 1973). They indicate that the coxae moved substantially, both in and out as well as back and forth, during production of the trace, since these impressions are in contact along their edges (Bergström, 1973). If the coxae were actually this large, the appendages could not have been rotated to effect the digging stroke necessary in the production of *Cruziana* and *Rusophycus* (Bergström, 1973; see figure 10).

Birkenmajer and Brunton (1971) proposed that small *Rusophycus* could have been produced by current scour around a trilobite resting on the bottom rather than being actively dug out. However, Crimes (1975b) refuted this theory, by pointing out that while such a process would produce *Rusophycus* that gape down stream, towards the back of the trilobite (Birkenmajer and Brunton, 1971), most *Rusophycus* show independent evidence that the median groove widens towards the front of the trilobite and, in most cases, up stream.

Functional Ethology

Rusophycus represents a number of ethological types, as its wide range in morphology might suggest. Unfortunately, the mechanics of formation are not substantially different for these various ethological goals. Thus it is often difficult to determine the ethology of any particular specimen from its intrinsic morphology alone. This determination must often be made using the sedimentological and ecological context as well.

The original ethological interpretation of *Rusophycus* was that of a temporary resting trace (Crimes, 1970c, 1975b; Seilacher, 1970; Bergström, 1976). Some examples are probably the result of temporary shelters, especially very shallow specimens such as *Rusophycus parallelum* Bergström, 1970. However, Seilacher (1985) suggested that most *Rusophycus* are not simple resting traces as a medially directed digging stroke would be a very inefficient way to dig a pit as it piles sediment under the trace maker. Thus, there must have been some other purpose for most of these structures. Most ethological interpretations of *Rusophycus* fall into two broad categories: feeding and self-protection.

Feeding behaviours resulting in *Rusophycus* fall into three categories: hunting or accidental capture of large infauna (Bergström, 1973, 1980; Crimes, 1975b; Osgood and Drennen, 1975); detritus-feeding (Bergström, 1973, 1980; Whittington, 1980; Seilacher, 1985; Zell, 1988); and filter-feeding (Eldredge, 1971; Bergström, 1973; Stürmer and Bergström, 1973; Seilacher, 1985; Zell, 1988).

Deposit-feeding and macrofaunal predation, using the *Rusophycus* behaviour, involves the same mechanics as for *Cruziana*. Opposing gnathobases formed a ventro-median food groove, that pushed food forward to the mouth (Bergström, 1980; Whittington, 1980; Cisne, 1981; see Ichnogenus *Cruziana*). Cisne (1981) noted that the cephalic appendages of the trilobite *Triarthrus* were articulated so that the tips spread apart when pushed back and came together when pulled forward. Thus, they could have pulled food into the mouth after it was deposited on the sediment by the anterior trunk coxae. Food could also have been sucked into the mouth by expansion of the glabellar gut (Seilacher, 1985). Detritus could have been transported to the ventro-median food groove using by a scraping action of the setae at the end of the telopodites. Whittington (1980) and Whittington and Almond (1987) claimed that the *Rusophycus* behaviour is better adapted to deposit-feeding than *Cruziana* since the appendages could have worked more efficiently without having to supply a propulsive force and gnathobases could have been held at an optimum orientation for moving food particles.

This process could also have handled large, and even live animals. Leg spines could have held large food items and live prey against the gnathobases which could have ripped the large particles apart as they pushed the pieces forward (Bergström, 1973). Seilacher (1962) proposed that highly setiferous telopodites could have formed a basket trap for trapping and holding large prey animals until they could be dismembered by the gnathobases. Stürmer and Bergström (1973) proposed that medially directed processes on the cephalic coxae of *Phacops* could have been used as jaws to shred food and push it into the mouth.

Bergström (1973) and Osgood and Drennen (1975) both figured *Planolites* terminating at the bottom of *Rusophycus*, suggesting that the *Rusophycus* trace maker captured and ate the *Planolites* trace maker. In most cases, the capture of live prey was probably an accidental event in the course of more general deposit-feeding activities on the part of the *Rusophycus* trace maker. It is difficult to imagine how a trilobite could effectively locate a mobile infaunal prey organism accurately enough from the surface to dig down and capture it. The only situation in which active hunting of infauna seems plausible is in areas of dense, sessile infauna, such as areas of dense shaft dwelling filter-feeders, so that random excavations would likely be successful (see Baldwin, 1977a; Chapter 3, Unit 3).

Rusophycus pits could have been used for filter-feeding in one of two ways. One way would be to create a one way current with rear exites through a open, U-shaped burrow and strain material from the water column using more anterior exites (Seilacher, 1985). Another method would be to stir up material while making the *Rusophycus* pit and filter food particles from the suspended sediment using the exites (Eldredge, 1971; Stürmer and Bergström, 1973; Seilacher, 1985; Zell, 1988). Material could have been transferred to the ventro-median food groove either by ciliary action or by the telopodites.

Seilacher (1985) claimed that fine terrace lines along the ventral and dorsal surfaces of the carapace of benthic trilobites are indicative of a filter-feeding habit. The terraces have steep faces oriented that would have prevented sediment from collapsing into an open chamber formed under a burrowing trilobite (Seilacher, 1985). Such a chamber, open at both ends, could then have been used as a filter-feeding chamber (Seilacher, 1985). Fortey (1985) countered that these terraces are present on free swimming trilobites as well as in places on benthic trilobites that could not have come in contact with the sediment in Seilacher's (1985) model. Thus, the presence of such terraces can not be used to assume that a particular trilobite taxon filter-fed in the manner described by Seilacher (Fortey, 1985).

The use of the *Rusophycus* generating behaviour for protective purposes could have involved a number of situations. Trilobites could have burrowed for protection of the ventral surface, especially in non-enrolling trilobites (Bergström, 1973; Osgood and Drennen, 1975). The *Rusophycus* behaviour could also have been used as a rapid escape mechanism from predators (Osgood and Drennen, 1975), especially in deep forms with oblique scratch marks. *Rusophycus* could also have been used as temporary shelter from inclement conditions (Crimes, 1970c; Bergström ,1973) and would have been especially useful in settings where conditions fluctuated regularly, such as tidally dominated environments. The trace makers could have burrowed to avoid being carried off by tidal currents or to avoid the effects of exposure during low tide. During high tide, or slack periods near low tide, they would have been able to move around on the sediment. Deep *Rusophycus* could also have been used as aestivation pits to allow the trace maker to survive prolonged inclement conditions.

Other interpretations of *Rusophycus* include semipermanent dwellings (Bergström, 1973; Goldring, 1985) and egg laying nests (Fenton and Fenton, 1937). In both cases one would expect much less regular scratch marks as a result of repetitious actions.

Environmental Associations

A survey of the literature shows that the environmental distribution of *Rusophycus* is not significantly different from that of *Cruziana*, either with respect to the gross environment or to particular physical conditions in the sediment or water column (Crimes, 1970c; Osgood and Drennen, 1975; Crimes *et al.*, 1977; Baldwin, 1977a; Fillion and Pickerill, 1984; and others; see Ichnogenus *Cruziana*, Environmental Associations). This supports the notion that *Cruziana* and and *Rusophycus* are both components of a complex repertoire of behaviour patterns that trilobites utilised as part of their every-day life (Crimes, 1970c). Crimes (1970c) noted a slightly higher proportion of *Cruziana* over *Rusophycus* in higher energy settings. This is possibly a response to food distribution. In higher energy settings, organic detritus is likely to be more evenly distributed while in quiet water settings, any patches of detritus are more likely to remain as discrete patches. Thus, a grazing behaviour like *Cruziana* would be more appropriate in higher energy conditions and a browsing behaviour like *Rusophycus* would be more appropriate in lower energy conditions.

Rusophycus avalonensis Crimes and Anderson, 1985

plate 26a, e, f

=*Cruziana fasciculata* Seilacher, 1970 (in part) (Crimes and Anderson, 1985)

Diagnosis

Rusophycus consisting of fine scratch marks in bundles of 5 or more. Bundles are flat near the margins of the trace and bunch up and curve back near the median groove. They are transverse at the front end and become more oblique towards the back. (after Seilacher, 1970; Crimes and Anderson, 1985)

Stratigraphic Range

Rusophycus avalonensis is known from Early Cambrian deposits (Seilacher, 1970; Crimes and Anderson, 1985).

Occurrence

Specimens of *Rusophycus avalonensis* were found in unit 2 and on float at Lake O'Hara.

Description

Specimens consist of two lobes separated by a distinct median groove or gap. There are two different forms conforming to the diagnosis of this ichnospecies. The length to width ratio (shape factor) was 1.4 in both forms. Form A consists of shallow specimens, less than 7 mm in relief (plate 26f). The lobes have straight, longitudinal outer edges and curved inner edges so that there is a median groove at the midsection of the trace fossil and a median gap at each end, the posterior one of which is longer. Scratch marks are long, fine, regularly spaced and range from oblique at the front end to near longitudinal at the back. There is a tendency for the scratch marks to become bundled towards the median groove at the front of the trace fossil.

Form B consists of long ellipsoidal lobes, with straight lateral and medial sides over most of their length (plate 26a, e). They average 20–30 mm in width and are separated by a 1–2 mm wide median gap. The maximum lobe height is at the mid section, up to 15 mm. Scratch marks are fine, regularly spaced, oblique, and become more oblique and tightly bundled in the median groove.

Discussion

Seilacher (1970) erected *Cruziana fasciculata* for specimens of both *Cruziana* and *Rusophycus* with the characteristic scratch mark pattern. Crimes *et al.* (1977), however, restricted *C. fasciculata* to long furrows. Crimes and Anderson (1985) erected *Rusophycus avalonensis* for the *Rusophycus* specimens of Seilacher's (1970) material. *Rusophycus avalonensis* is characterised by bundles of 5–6 fine, subequal scratch marks (Seilacher, 1970). The bundles are transverse anteriorly and grade back to 30^{o} from longitudinal (Seilacher, 1970). All scratch marks curve back slightly towards the median groove (Seilacher, 1970). Seilacher's (1970, figure 7-3) drawing shows that the lobes have bulbous anterior ends that slope and taper back. The general form of *Rusophycus avalonensis* is quite variable, ranging from the typical shape figured by Seilacher (1970) to vague pairs of scratch mark bundles (Crimes and Anderson, 1985). Most forms are shallow (Crimes and Anderson, 1985), however, some high relief specimens are known. For example, Alpert (1976) described circular to elliptical, paired lobes separated by a distinct median gap as in *Rusophycus barbata* Seilacher, 1970, however, the scratch mark pattern is closer to that of *Rusophycus avalonensis* (Crimes and Anderson, 1985)

The scratch marks of *Cruziana fasciculata* and *Rusophycus avalonensis* are thought to be produced either by multiclawed telopodites (Seilacher, 1970; Crimes, 1975a) or exites (Bergström, 1972, 1973). However, no known telopodite or exite reconstructions could have produced these scratch marks (Seilacher, 1985; Müller and Walossek, 1987). It is unlikely that these fine scratch marks could have caused by setae along the side of the telopodite, since these would be lifted up off the sediment as the telopodite tip was brought close to the median line (Crimes, 1975a). Moreover, to produce wide sets of transverse scratch marks by this method, the distal few podomeres of the telopodite would have had to be flexed laterally by nearly 90°. None of the known appendage reconstructions have podomere joints that could be flexed in the lateral plane to any significant degree (Whittington, 1980; Müller and Walossek, 1987). The medial bundling of fan like sets fine scratch marks suggests that the causative appendage was a broad fan of spines that was held in a constant orientation throughout the digging stroke (figure 12). This probably served to deposit whatever detritus had been collected, near the gnathobases.

The plan view outline of *Rusophycus avalonensis* form A from this study is similar to the drawing drawing of *Cruziana fasciculata* in Seilacher (1970). Form B resembles the general form of the *R. avalonensis* (*Rusophycus barbata*) described by Alpert (1976).

Rusophycus bilobatum Vanuxem, 1842

plate 25d, e

Diagnosis

Rusophycus with elongate, straight sided lobes, tapering at each end, and covered with coarse, close and irregularly spaced, transverse scratch marks in bunches of up to 3 (after Osgood and Drennen, 1975; Landing and Brett, 1987).

Stratigraphic Range

Rusophycus bilobatum is known from Silurian deposits (Osgood and Drennen, 1975) although material reported as *Rusophycus* ichnosp. from Lower Cambrian strata (Fritz *et al.*, 1983) is identical to Osgood and Drennen's (1975) material.

Occurrence

Most specimens of *Rusophycus bilobatum* were recovered from unit 2, subunit 3b, 4m to 4y, 6c, and 6g. A small number were found at Moraine Lake and Lake O'Hara.

Description

There are two distinct forms that conform to the diagnosis of this ichnospecies. Form A consists of two moderate relief lobes separated by a deep median groove that is best developed at the front of the trace (plate 25d). The lobes are well rounded at the front end and taper and slope back slightly. In plan view, the traces are heart shaped, with a shape factor averaging 1.3. Scratch marks are straight, coarse, paired, and near transverse, becoming more oblique towards the back end.

Form B consists of two flat to slightly rounded, low relief lobes separated by a narrow median groove (plate 25c). The shape factor is approximately 1 with a rectangular shape in plan view. The scratch marks are coarse and paired, and grade from transverse at the front to oblique at the back of some specimens.

Discussion

Rusophycus bilobatum consists of wide, flat topped lobes with coarse, transverse scratch marks (after Osgood and Drennen, 1975). The close spaced, sub-parallel scratch marks impart an irregular appearance to the trace (Osgood and Drennen, 1975, plates 1-3). The median groove is very narrow and shallow (Osgood and Drennen, 1975). The general shape and outline of *Rusophycus bilobatum* is quite variable, probably the result a number of different taxa of trace makers (see Osgood and Drennen, 1975). Most forms are rectangular and straight-sided in plan view with little or no tapering and very little bulbousness to the lobe terminations (Osgood, and Drennen, 1975). The side view shape varies from flat to sloping or arcuate (Osgood and Drennen, 1975). While most specimens are of low to moderate relief, some specimens have short vertical sides (Osgood and Drennen, 1975).

The close spaced, irregular, transverse scratch marks suggest that the substrate was disrupted as much as possible. Thus, this ichnospecies was most likely produced as a shallow deposit-feeding structure. *Rusophycus bilobatum* is one ichnospecies that is sometimes seen with terminating *Planolites* burrows, suggesting that the *Planolites* trace maker was eaten by the trilobite (Osgood and Drennen, 1975). Both forms from this study fall within the range of morphotypes in Osgood and Drennen's (1975) specimens. *Rusophycus bilobatum* is one of the most common ichnospecies in this study. This most likely the result of the fact that it does not represent any specialised behaviour pattern.

Rusophycus carinatus (Seilacher, 1970)
plate 27f

=*Cruziana carinata* Seilacher, 1970 (Crimes *et al.*, 1977)

Diagnosis

Rusophycus with elongate, divergent lobes composed of an inner lobe with coarse, oblique scratch marks and an outer lobe with fine, longitudinal brush marks (after Seilacher, 1970).

Stratigraphic Range

Rusophycus carinatus is known from the Lower Cambrian (Seilacher, 1970; Crimes *et al.*, 1977).

Occurrence

A single specimen of *Rusophycus carinatus* was found on float in unit 4. The lithology of the sample is indicative of the upper part of the unit, above subunit 4m.

Description

The trace fossil consists of a set of low relief medial lobes and 5 mm high, well rounded lateral lobes. Each lateral and medial lobe pair is 20 mm wide and 100 mm long. The median gap varies from 2 mm wide at the back end to 30 mm at the front. The medial lobes are made up of coarse, smooth scratch marks, 10–20^{o} to the trend of the lobes. These scratch marks are very irregular in thickness and length. The lateral lobes are covered with very fine, longitudinal brush marks.

Discussion

Rusophycus carinatus is characterised by two features: the presence of lateral lobes with fine, longitudinal brush marks along the whole length of the trace, and the large shape factor (Seilacher, 1970; Crimes *et al.*, 1977). The marked dichotomy between the coarse, medial lobe scratch marks and lateral lobe brush marks indicates that the lateral lobes must have been produced by the exite branches (Seilacher, 1970; Crimes *et al.*, 1977). To produce long, longitudinal lineations the exite fringe must have hung down outside the telopodites and have been able to swing freely. The featureless median gap suggests that this was a shallow trace since there are no impressions of ventral body parts to be seen in any examples (Seilacher, 1970; Crimes *et al.*, 1977; plate 27f).

The elongate shape of this ichnospecies indicates a much longer trace maker than those responsible for most other *Rusophycus* (Osgood, 1970; Seilacher, 1970; Baldwin, 1977a; Crimes *et al.*, 1977). This unusual shape is found in all three occurrences of *R. carinatus* (Seilacher, 1970; Crimes *et al.*, 1977; plate 27f).

Rusophycus cf. *cerecedensis* Crimes *et al.*, 1977
plates 25f; 28b

Diagnosis

Shallow to deep, well defined posteriorly tapering bilobate traces with lobes that meeting centrally and are covered with claw markings which are coarse, bunched in pairs, and typically run approximately transversely in the anterior part of the trace but form a lower V-angle in the middle and posterior parts (Crimes *et al*., 1977).

Stratigraphic Range

Rusophycus cerecedensis is known from the Lower Cambrian (Crimes *et al*., 1977).

Occurrence

The majority of specimens were found on float at Moraine Lake and Lake O'Hara, with a single occurrence from unit 6.

Description

Specimens consist of well rounded, moderate relief lobes separated by a narrow median gap that increases in width towards the back of the trace. The lobes are bulbous at the front and taper and slope back. In plan view the shape is similar to *R. jenningsi* and *R. bilobatum* form A, but with a larger shape factor, approximately 2. Scratch marks are coarse, well spaced, strongly paired, straight, and range from oblique to near transverse at the front.

Discussion

The specimens from this study match the diagnosis of Crimes *et al.* (1977) exactly. The scratch marks in these specimens are much sharper than those of Crimes *et al.* (1977). This indicates that these specimens were emplaced in a more cohesive substrate. *Rusophycus cerecedensis* is similar to *Rusophycus dispar* (Crimes *et al*., 1977) except that there is no sharp transition between the anterior and posterior scratch marks. As well, the lobe structure of *Rusophycus cerecedensis* is much more clearly defined (Crimes *et al*., 1977), as it is in the specimens from this study. The scratch mark pattern of *R. cerecedensis* is also unique in the regular spacing of the markings.

The well defined scratch marks of *R. cerecedensis* in this study are indicative of a strongly cohesive substrate. This ichnotaxon is most common in unit 6 and at Lake O'Hara, both of which are characterised by sediments and other ichnotaxa indicative of firm, cohesive substrates, if not the *Glossifungites* ichnofacies. The similar *R. bilobatum*, on the other hand, is most common at Redoubt Mountain and Moraine Lake, which were characterised by much softer substrates. *R. cerecedensis* may represent a modified form of the *R. bilobatum* behaviour, produced in cohesive substrates

Rusophycus ?dispar Linnarsson, 1869

plate 28d

=*Cruziana dispar* Seilacher, 1970

Diagnosis

Rusophycus with coarse, oblique, bundles of unequal scratch marks. Anterior and posterior scratch marks differ in both the orientation and strength of impression, with a sharp demarcation between the two types. Anterior V-marks may open back. (after Seilacher, 1970)

Stratigraphic Range

Rusophycus dispar is known from the Lower Cambrian (Seilacher, 1970; Alpert, 1976).

Occurrence

Rusophycus ?dispar was found on float at Moraine Lake and Lake O'Hara.

Description

Specimens consist of moustache like sets of long, gently curved, coarse scratch marks separated by a distinct median groove. They are preserved on the base of thin sandstones overlying thin shale horizons.

Discussion

The scratch mark pattern of specimens of *Rusophycus ?dispar* from this study are similar to those of *R. bilobatum* except that the scratch marks occurred as isolated, moustache-like bundles, common in *R. dispar* (Seilacher, 1970) rather than on well defined lobes. A point was made of distinguishing these specimens from those of *R. bilobatum* because the moustache-like configuration of the former, without any trace of the rest of the trace maker's appendages, suggests that the trace maker dug through the casting bed to reach the mud layer into which the trace was formed (Seilacher, 1970). This is a significant ethological feature and merits separate ichnotaxonomic treatment. *Rusophycus dispar* is an extremely variable ichnospecies however, ranging from shallow traces, as the ones in this study, to extremely deep, steep-sided pits (Seilacher, 1970). The one uniting feature is that the actions of the anterior appendages are distinct from those of the posterior appendages with respect to direction of movement and strength of impression, with a sharp demarcation between the resulting sets of scratch marks (Seilacher, 1970). Thus, the ethological distinction used to separate specimens of *R. ?dispar* from *R. bilobatum* in this study, while typical of *R. dispar*, is not a diagnostic feature.

Rusophycus eutendorfensis (Link, 1942)

plate 27a, b, c

=*Arenicola didyma* Salter, 1856 (*Partim*) (Seilacher, 1953)
=*Isopodichnus* Bornemann, 1889 (Bromley and Asgaard, 1979)
=*Isopodichnus eutendorfensis* Link, 1942 (Bromley and Asgaard, 1979)
=*Cruziana* (*Rusophycus*) *didyma* (Salter) Seilacher, 1953, 1954, 1955; Lessertisseur, 1955 (Bromley and Asgaard, 1979)

Diagnosis

Small *Rusophycus*, 0.8–14 mm in width and length. The gross morphology and scratch mark detail are not diagnostic (Bromley and Asgaard, 1979).

Stratigraphic Range

Rusophycus eutendorfensis is known from Early Cambrian to Triassic deposits (Crimes, 1975a; Bromley and Asgaard, 1979).

Occurrence

Specimens of *Rusophycus eutendorfensis* were found in subunits 4t, 4x, 6a, and 6c, and on float at Moraine Lake and Lake O'Hara. The majority of specimens were found in subunit 6a.

Description

There are two forms that conform to the diagnosis of this ichnospecies. Both are most common in thinly interbedded quartzite and shale laminae, less than 5 mm thick. Form A consists of less than 5 mm wide, less than 2 mm high, oval lobes separated by a median groove that often gapes up to 2 mm at one end (plate 27c). The shape factor averages 2. Scratch marks are straight, transverse to slightly oblique, and very fine, approximately 4 per millimetre. They span the width of the lobe. Form B consists of straight sided lobes, less than 5 mm wide, separated by a thin median groove (plate 27a, b). The lobes slope down at either end with a maximum height of up to 4 mm at the midsection. The shape factor is approximately 1–1.5 and the trace fossils taper slightly at each end. Traces are often serially arranged in groups of up to 10. Scratch mark detail is poorly preserved.

Discussion

The most common practice has been to place all small forms of *Rusophycus* within the ichnogenus *Isopodichnus* (Hakes, 1985). This scheme is not followed in this study (see Ichnogenus *Cruziana*, Ichnotaxonomy). The various forms of small *Rusophycus* have been assigned to *Rusophycus eutendorfensis*, following Bromley and Asgaard (1979) and Fillion and Pickerill (1984). *Rusophycus eutendorfensis* contains a number of distinct forms that should probably be separated in the nomenclature. However, there are large a number of different forms, many of which are identical, except for size, to other recognised ichnospecies of *Rusophycus*. Thus, any attempt to split up *Rusophycus eutendorfensis* without a detailed revision of all known forms would only create more confusion.

Rusophycus eutendorfensis has been differentiated from other ichnospecies of *Rusophycus* by its small size, on the assumption that this indicates a different trace maker (Crimes, 1970c). However, both Radwanski and Roniewicz (1963) and Crimes (1970c) noted large collections of *Rusophycus* in which there is a continuous intergradation in size between specimens of *R. didymus* (=*R. eutendorfensis*) and *R. bilobatum*. The scratch mark pattern and shape factor are the same throughout these collections. Thus, the *R. didymus* and *R. bilobatum* were made by different ontogenetic stages of the same species of trilobites, all performing the same activity (Crimes, 1970c). This is interesting because it indicates that some benthic trilobites adopted a benthic habit very early in their life cycle. These observations suggest that "*Isopodichnus*" forms of *Cruziana* and *Rusophycus* should probably be lumped into the various ichnospecies of larger forms of *Cruziana* and *Rusophycus* with which they have morphological affinities (Crimes, 1970c).

The specimens of *R. eutendorfensis* in this study are similar to a number of other ichnospecies. *R. eutendorfensis* form A, with its well defined, transverse scratch marks, has forms that correspond to the diagnoses of *Rusophycus parallelum* and *Rusophycus cerecedensis*. The lobe structure of form B resembles that of *Rusophycus bilobatum* and *Rusophycus* ichnosp. 3. The largest specimen is just less than 25% of the size of the smallest *R*. ichnosp. 3. Thus, *Rusophycus eutendorfensis* forms A and B probably represent the activities of the early life stages of the same trilobites that produced *Rusophycus cerecedensis*, *R. parallelum*, and *R*. ichnosp. 3 as adults.

Rusophycus eutendorfensis is, for the most part, restricted to thinly interbedded sandstones and shale, suggesting an environmental preference for more quiet water conditions on the part of smaller arthropods (see Ichnogenus *Cruziana*, Environmental Associations). The serially arranged specimens of form B are the result of one trace maker moving along the sediment surface and periodically creating small excavations, possibly to deposit-feed off surface detritus.

Rusophycus jenningsi (Fenton and Fenton, 1937)
plate 26b, c, d

=*Cruziana jenningsi* Fenton and Fenton, 1937

Diagnosis

Rusophycus consisting of two high relief lobes with the front end and both sides made up of a near vertical face. The top is strongly bilobed and slopes back to the back end of the trace. Scratch marks are coarse and bundled; near transverse at the steep end and becoming finer and more oblique towards the shallow end. The vertical face has smooth horizontal ridges that may curve down towards at the back end. (after Fenton and Fenton, 1937)

Stratigraphic Range

Rusophycus jenningsi is known to range throughout the Cambrian (Seilacher, 1970); although some of this material may not be *R. jenningsi* (see below).

Occurrence

All specimens were found on a single float block at Lake O'Hara.

Description

The specimens consist of bulbous, well rounded lobes that slope and tapered back. In plan view the structures have an elongate heart shape with a shape ratio of 1–1.5. The front and forward sides of the traces are vertical faces, up to 40 mm high, with horizontal ridges that curve down at either end (plate 26b). The median groove is deepest at the front of the trace, up to 5 mm deep. Scratch marks are coarse and span the width of the lobes. They are near transverse at the edge of the lobes and curve back towards longitudinal as they approach the median groove. Scratch marks become finer and more longitudinal towards the back with a sharp transition in some specimens (plate 26c). The grouping of scratch marks is difficult to determine but they appear to become bundled towards the median groove.

Discussion

Rusophycus jenningsi consists of deep casts with well developed bilobed tops that slope gently back, and a vertical front and sides (Fenton and Fenton, 1937). The lobes are covered with scratch marks which consist of narrow fans of fine, parallel scratches that coalesce into tight, high relief bundles (Fenton and Fenton, 1937). This is similar to the pattern in *Rusophycus avalonensis* although the marks are coarser. The similar, and distinct scratch mark pattern along with the similarity in plan view shape suggest that the same taxon of trace maker was responsible for both. The scratch marks in *R. jenningsi* become finer and more oblique down the slope with a sharp transition approximately half way down the slope (Fenton and Fenton, 1937). The most diagnostic features are the vertical front and sides, ornamented with horizontal ridges that curve toward the base of the trace fossil as they approach its sloping end (Fenton and Fenton, 1937).

Rusophycus jenningsi is interpreted to be the result of deep excavations made by a combination of shovelling with the anterior margin of the cephalon, producing the horizontal ridges along the front and side face, and digging with the appendages, producing the scratch-marked lobes (Fenton and Fenton, 1937). The multiple ridges on *Rusophycus jenningsi* indicate that a number of shovelling actions were involved in the excavation of the front of this trace. The steep slope and unique excavation style of this ichnotaxon suggest that its purpose was to do more than just to bury the trace maker or search for food (Fenton and Fenton, 1937). However, Fenton and Fenton's contention that the traces were dug as egg laying pits, although possible, is without any supporting evidence.

The scratch marks in some specimens show a sharp dividing line between coarse anterior scratch marks and finer posterior scratch marks, similar to Fenton and Fenton's (1937, figures 1 and 2) drawings. The scratch mark pattern does not change substantially across this line, thus, Bergstrom's (1973) contention the these two zones were produced by different appendage branches is not supported. The decrease in scratch mark impression is probably due to a decrease in appendage size toward the back of trace maker (Seilacher, 1985). The medial clumping of scratch marks is likely due to the same mechanism as in *Rusophycus avalonensis*. There is no medial decrease in scratch mark number to supports Bergström's (1973) hypothesis that the clumping is due to the marginal setae along the length of the telopodite being lifted off the sediment as the appendage is flexed inward, causing an apparent bunching of the scratch marks.

Rusophycus jenningsi must have been dug in firm, cohesive muds for the walls of the burrow to have withstood collapse (Fenton and Fenton, 1937). This inference is supported by the presence of *Palaeophycus striatus*, with well preserved striae, associated with the specimens from this study.

Bergström (1976) assigned several specimens to *R. jenningsi* based on their similarity with Fenton and Fenton's (1937) *Cruziana (=Rusophycus) irregularis*, and Seilacher's (1970) synonymising of *Cruziana irregularis* with *Cruziana jenningsi*. However, Fenton and Fenton's (1937) *Cruziana irregularis* is a much shallower burrow than *Rusophycus jenningsi*, has more regular scratch marks that do not bunch together in the median groove, and lacks the steep front and sides (Fenton and Fenton, 1937). Seilacher (1970) had no justification for combining *C. irregularis* under *C. jenningsi* except that the trace maker was presumed to be the same for both ichnospecies. There is, however, very little, if any, evidence to suggest that Bergström's "*Rusophycus jenningsi*" were produced by the same taxon of trilobites that produced Fenton and Fenton's material given the geographic separation of the two areas at that period in geologic time. *Cruziana irregularis* and Bergström's (1976) *Rusophycus jenningsi* should probably be assigned to *Rusophycus cerecedensis* based on the similarity of the scratch mark patterns to Crimes *et al.*'s (1977) diagnosis. This is an example of the confusion that can be caused by relying on trace maker identity as a key to the classification of trace fossils.

Pickerill (1977) assigned two rather poorly preserved specimens from the Caradoc (upper Ordovician) to *Rusophycus jenningsi*. However, none of the diagnostic features of Fenton and Fenton's material are preserved in Pickerill's specimens. Judging from Pickerill's description and figure, these specimens would be more properly referred to as ?*Rusophycus*.

Rusophycus navicella (Fenton and Fenton, 1937)
plate 25c

=*Cruziana navicella* Fenton and Fenton, 1937

Diagnosis

Long *Rusophycus* with irregular, low angle curves and a poorly defined lobe structure. One end is steep and blunt, the other slopes gently down to the bedding surface. The top of the structure is covered with irregularly oriented sets of fine, mutually parallel scratch marks. (after Fenton and Fenton, 1937)

Stratigraphic Range

Rusophycus navicella is known only from Early Cambrian deposits (Fenton and Fenton, 1937).

Occurrence

Rusophycus navicella was found on float in unit 2 and subunit 6c.

Description

The specimens from unit 6 consist of high relief, steep sided and fronted, flat topped mounds with poorly developed median grooves. The structures are up to 3 times as long as they are wide with slight bends along length. Scratch marks are fine, long, straight, and organised into small sets whose orientations vary from transverse to longitudinal along the lobes.

Specimens from unit 2 consist of high relief mounds with poorly developed lobes. The maximum relief is at one end and the trace fossils taper and slope back from this. Scratch marks are made up of what seem to be randomly distributed and oriented sets of short, fine, parallel scratch marks.

Discussion

Rusophycus navicella consists of short, pocket-like burrows covered with irregularly arranged sets of short, parallel scratch marks (Fenton and Fenton, 1937). These suggest that the trace maker turned about a great deal while constructing the burrow. Therefore, the burrow must have been significantly larger than the trace maker itself (Fenton and Fenton, 1937). The smoothness of the burrow walls suggests a long period of habitation, perhaps a semipermanent dwelling, rather than an egg laying nest or feeding pit as proposed by Fenton and Fenton (1937). The wide, open, unlined burrows must have been produced in a strongly cohesive sediment to have resisted collapse.

Seilacher (1970) provisionally grouped *Rusophycus navicella* under *Cruziana* (=*Rusophycus*) *jenningsi* based on a similarity in scratch mark pattern. However, the overall form and inferred mode of construction of *R. navicella* is profoundly different from that of *Rusophycus jenningsi*, thus the two should be kept separate. The morphology and inferred mode of construction of *R. navicella* are profoundly different from any other *Rusophycus*, in fact, and bear a distinct similarity to those of *Trichophycus*.

One large specimen from this study matches figures 5 and 6 of Fenton and Fenton (1937) except that the scratch marks are some what finer. The smaller forms from unit 2 consist of irregular mounds, sloping gently in one direction and without the elongate pocket morphology of the larger specimen. They may represent incipient *R. navicella* structures that were abandoned before completion. They bear a superficial resemblance to *Rusophycus radwanski* Alpert, 1976 but the lobe structure is not as well defined.

Rusophycus cf. *parallelum* Bergström, 1970

plate 25a, b

Diagnosis

Low relief *Rusophycus* with elongate, straight and parallel sided lobes covered with straight, paired scratch marks (Bergström, 1970).

Stratigraphic Range

Rusophycus parallelum is known only from Early Cambrian deposits (Bergström, 1970).

Occurrence

Rusophycus parallelum was found in subunits 2b and 2g, and on float at Moraine Lake.

Description

Specimens consist of straight sided, well rounded lobes separated by a narrow median groove. The shape factor is approximately 1.2 to 1.3 and the length varies from 25–50 mm. The lobes slope down at either end with a maximum relief of up to 15 mm at the midsection. Scratch marks are coarse, paired, and oblique to transverse, with a constant angle along the length of the trace.

Discussion

Rusophycus parallelum is distinguished by low relief, straight sided, parallel lobes covered by dense, transverse to oblique, paired scratch marks (Bergström, 1970). Bergström's two specimens were found on the base of a sandstone slab which casts a symmetrically rippled surface. One of the specimens follows the ripple topography without changing relief (Bergström, 1970). Thus, these traces must have been extremely shallow and were probably simple resting traces (Bergström, 1970), constructed to avoid being buffeted by currents or wave action.

The specimens from this study are similar to Bergström's diagnosis except that the relief is 2–3 times that of Bergström's specimens relative to their width and length. Thus, the specimens from this study may be more than just temporary resting excavations; possibly the result of deposit-feeding. *Rusophycus parallelum* is only known from Bergström's (1970) two specimens, thus there is no substantial data base with which to compare the morphology of the specimens from this study. The specimens from this study are similar to those of *R. cerecedensis* except for the plan view shape and the strength of impression of the scratch marks. They are assigned to *R. parallelum* because the plan view shape of the lobes and the scratch mark pattern matches Bergström's diagnosis. However, the plan view shape is controlled more by the identity of the trace maker rather than its behaviour. The ethology of Bergström's specimens and the specimens from this study may be quite different.

Rusophycus rugosa d'Orbigny, 1842
plate 28e, f

Diagnosis

Rusophycus consisting of two lobes covered with sets of short, straight, parallel, near longitudinal scratch marks. The sets span the width of the lobes, with approximately 10–12 scratch marks across each lobe. Successive sets are separated by near transverse ridges or gaps. (after Seilacher, 1970; Baldwin, 1977a)

Stratigraphic Range

Rusophycus rugosa is common from the Arenig to the Llandeilo, although it may range into the Tremadoc (Crimes, 1970b; Crimes, 1975a).

Occurrence

Rusophycus rugosa was found in subunit 2o and in two undetermined horizons in unit 2.

Description

Specimens consist of bilobed pits with steep to near vertical front faces and bilobed tops that slope gently back. The median groove is not always distinct. Scratch marks are organised into sets of 4–6 mm long, mutually parallel, near longitudinal marks. These are regularly spaced about 1 mm apart with 10–12 marks across each lobe. Successive scratch mark sets are separated by near transverse ridges or depressions, 1–2 mm wide.

Discussion

The mechanics of formation for *Rusophycus rugosa* is discussed in detail under *Cruziana rugosa*. The short, parallel scratch mark sets must have resulted from digging strokes by an comb-like appendage. The presence of these scratch marks along the entire length of the specimens indicates that they were the only appendage used in digging. Thus, in this type of trilobite, the comb-like appendages were capable of exerting a significant force against the sediment and must have been the dominant appendage along the entire length of the trace maker. In spite of this unique appendage structure, Seilacher (1970) and Crimes (1975a) consider this ichnospecies to have been produced by trilobites.

Rusophycus rugosa is quite rare compared to *Cruziana rugosa*, although most *Cruziana rugosa* are little more than elongate *Rusophycus* (Seilacher, 1970). The trace maker of rugosa-type traces did not commonly use this mode of action to create either long furrows or deep pits. The short digging strokes were probably not very effective for excavating sediment or for locomotion. The steep front face in the specimens in this study suggests that the cephalon was used to help excavate sediment in a manner similar to that used in *Rusophycus jenningsi*.

Rusophycus ichnosp. 1

plate 28c

Occurrence

A single specimen of *Rusophycus* ichnosp. 1 was found in subunit 6c.

Description

The specimen forms a broad "U" with 9 mm wide lobes that are joined together at one end to surround a 15 mm wide, featureless median gap on three sides. The specimen is 34 mm long and less than 1 mm in relief. Scratch marks vary from 45^{0} where the arms join to almost transverse along the arms of the U. The oblique scratches slant in and back towards the joined end and are finer than the more transverse marks along the rest of the lobes.

Discussion

This single specimen is little more than a set of surface scratches. It probably resulted from an arthropod that briefly touched down on the surface after floating or swimming. The broad U-shape probably results from the fact that trace maker's appendages were much shorter towards the posterior and thus; could not extend as far out as the more anterior appendages.

Rusophycus ichnosp. 2

plate 28a

Occurrence

Rusophycus ichnosp. 2 was found in subunits 4r, 4s, 6a, and 6c, and on float at Moraine Lake and Lake O'Hara.

Description

Specimens consist of long, straight sided lobes separated by a 1–3 mm wide median gap. The shape factor varies from 2–3 and width varies from 7–57 mm. Scratch marks are coarse, paired, straight to C-shaped in plan view, and vary from transverse to oblique.

Discussion

The extreme length and straight sides of these specimens suggest that some degree of forward motion was involved in their production. They must be a result of trilobites briefly furrowing down into the sediment while moving along the sediment surface. No evidence of intrastratal formation was found that would indicate that these traces are the bottom of shallow, U-shaped burrows as postulated by Goldring (1985) for similar *Rusophycus* specimens.

The wide variation in size and scratch mark pattern indicates that this form was produced by a number of different trilobite taxa. The smaller forms have C-shaped scratch marks, similar to *Cruziana problematica* while the larger ones have transverse scratch marks similar to *Rusophycus bilobatum* and *Cruziana* ichnosp. 4.

Rusophycus ichnosp. 3

plates 21a, b, d; 27d, e

=*Rusophycus gouini* (Baldwin, unpublished Ph.D. thesis, 1976)

Occurrence

Specimens of *Rusophycus* ichnosp. 3 were found in subunit 2d, 4s, 4w, 4x, and 4y, and on float in units 2, 6, and at Lake O'Hara.

Description

Specimens consist of narrow, high relief lobes with nearly triangular cross-sections. The shape factor averages 1.5 with lengths varying from 10–40 mm. Lobes are straight sided over most of their length and taper to a point at each end. High relief specimens have steep sided lobes and a narrow median grooves, others are less than 5 mm high and slope gently down on all sides. The low relief specimens have median gaps from 1–5 mm wide, often gaping at one end. Scratch marks are fine and bundled in groups about 3–4, which run obliquely to nearly longitudinal across the width of the lobes.

Discussion

This form is commonly found along with *Cruziana* ichnosp. 1 and has the same bunched, longitudinal scratch marks. Thus, it was probably made by the same type of trilobite. The presence of the same scratch mark pattern indicates that the multiclawed appendage that was dragged along in *Cruziana* ichnosp. 1 was capable of excavating sediment in *Rusophycus* ichnosp. 3. The cephalon could not have assisted in the excavation of this trace as the median groove is too deep.

This form of *Rusophycus* is common in western North America as *Rusophycus* sp. (Young, 1972; Alpert, 1976) and in Spain as "*Rusophycus gouini*" (Baldwin, 1976).

Ichnogenus *Skolithos* Haldeman, 1840

?=*Monocraterion* Torell, 1870 (Hallam and Swett, 1966; Goodwin and Anderson, 1974)

Type Ichnospecies

Fucoides linearis Haldeman, 1840

Diagnosis

Simple, non-branching, vertical to steeply inclined, cylindrical to subcylindrical simple tubes. Walls may be smooth, rough, or annulate and may or may not be lined. Diameter can vary slightly along length as can the orientation. The infill is structureless. (after Alpert, 1974)

Stratigraphic Range

Skolithos is known from the upper Precambrian to the Recent (Crimes and Germs 1982; Crimes, 1987).

Discussion

Skolithos consists of simple, non-branching, cylindrical to subcylindrical, vertical burrows. Burrows vary from 1–30 mm in diameter and and up to 1 m or more in length (Hallam and Swett, 1966; Häntzschel, 1975). Although slight local variations in diameter and orientation can occur, the tubes are generally straight, vertical, and of constant diameter over their whole length. Dark coloured wall linings may be present. The burrow infill is generally structureless but may exhibit a passive meniscus infill structure. (after Alpert, 1974)

Skolithos is interpreted to be infilled dwelling burrows, and are most commonly attributed to filter-feeding organisms; generally annelids and phoronids (Alpert, 1974; Miller and Knox, 1985). In modern settings, most *Skolithos* making organisms are vermiform suspension-feeders, however, some deposit-feeders, maldanid polychaetes for example, produce similar burrows (Miller and Knox, 1985).

In the modern, burrow linings consist of mucus or some form of cement (Goodwin and Anderson, 1974) in which may be incorporated small particles of shell or other material (Ekdale *et al.*, 1984). The mucus traps mud particles and results in a dark lining preserved in the fossil (S. Vossler, pers. comm., 1988). If no such material is available, no lining will be apparent in the ichnofossil even if it was present in the original burrow (S. Vossler, pers. comm., 1988). The lining functions to support the burrow and maintain the integrity of oxygenated water currents within the burrow (Goodwin and Anderson, 1974).

Deep burrows offer protection against temperature and salinity fluctuations (Goodwin and Anderson, 1974) since these parameters vary less within the sediment than in the water column (Ekdale *et al.*, 1984, figure 14-4). They also protect the trace maker against periodic emergence, and erosion of the sediment surface (Goodwin and Anderson, 1974). Thus, deep burrows are characteristic of fluctuating environments such as intertidal flats (Goodwin and Anderson, 1974). As the burrow of filter-feeders, *Skolithos* is indicative of high energy environments with abundant suspended food particles (Seilacher, 1967; Crimes, 1970; Goodwin and Anderson, 1974), high sediment stability, especially with respect to erosion and deposition, and a minimum of suspended sediment (Goodwin and Anderson, 1974). As living conditions and food supply improve, burrow spacing decreases (Goodwin and Anderson, 1974). As the burrow of sessile surface deposit-feeders, *Skolithos* is indicative of alternating high energy and prolonged low energy conditions resulting in a constant supply of organics settling onto the sediment.

The presence of dense clusters of shafts can increase the stability of the sediment, once the community of shaft making organisms has been established. Rigid shafts stabilise the substrate and rigid burrow linings that stick up above the sediment create a low velocity boundary layer above the sediment surface. The circulation of water through the shafts enhances the growth of filamentous algae within the surrounding sediment, as a result of changes in the pore water chemistry, and further stabilises the sediment. Thus, *Skolithos* making organisms can flourish as dense colonies under hydrodynamic conditions where individual shafts could not. One constraint on the presence of shaft dwelling filter-feeders, including *Skolithos*-makers, is the absence of motile deposit-feeders within the sediment. Deposit-feeders not only disrupt shaft construction and maintenance but they also create suspended, fine grained sediment which clogs filtering organs (Thayer, 1983).

The presence of *Skolithos* in thinly interbedded sandstones and shales should not be associated with the ichnofossils and sedimentary setting in which it is found unless distinct burrow tops are seen. The presence of shafts within such settings is often associated with thin sand layers that have subsequently been eroded away (Vossler and Pemberton, in press). These shafts can extend down into horizons that have been heavily bioturbated, but have no ecological relationship to the bioturbation (Vossler and Pemberton, in press).

While *Skolithos* is indicative of certain physical conditions, it is found in a wide range of environments (Miller and Knox, 1985). It is most commonly associated with shallow shelf and near shore marine environments (Seilacher, 1967; Crimes, 1970; Fillion and Pickerill, 1984). However, it has been found in rocks attributed to environments ranging from fresh water (Miller and Knox, 1985), flood plains and deposits with desiccation cracks (Ratcliffe and Fagerstrom, 1980; Pienkowski, 1985), marginal marine settings (Demathieu, 1985; Pienkowski, 1985), beach, intertidal flats, tidal channels (Goodwin and Anderson, 1974; Legg, 1985), and abyssal basins (Chamberlain, 1975; Miller and Knox, 1985).

Although *Skolithos* is generally easy to recognise in outcrop there are some situations where it can be misidentified. Isolated *Skolithos* are often seen in the thinly interbedded quartzites and shales of the recessive units at Redoubt Mountain. Some of these samples also contained horizontal burrows, especially *Palaeophycus*. The horizontal burrows often flex vertically, especially at high densities. When the surface of a slab intersects the vertical component of these burrows they can appear to be *Skolithos*. This problem is compounded by the frequent inability to see *Skolithos* in vertical section, even in pipe rock samples (plate 11d).

Skolithos annulatus Howell, 1957
plate 12d

Diagnosis

Cylindrical to subcylindrical, vertical burrows. Shaft diameter ranges up to 12 mm. Walls are distinct with smooth annulations 2–12 mm apart and 1–4 mm wide. (Alpert, 1974)

Occurrence

Skolithos annulatus is most common on float at Lake O'Hara, with a single find in subunit 3a.

Description

Specimens consist of 5–10 mm diameter, apparently unlined, quartzite infilled shafts with distinct annulations. The annulations are approximately 1 mm wide and project about 0.5–1 mm out from the shaft wall. Their spacing is irregular but averages about 1 mm.

Shaft lengths are indeterminate. Specimens are preserved as endichnia in substrates ranging from flaser bedded quartzites to thinly interbedded quartzites and hard, beige shales. The density of these shafts is less than 1 shaft per 100 cm^2.

Discussion

The function and formation of the annular rings ornamenting these burrows is unknown. Since the burrows are unlined it does not seem likely that the rings were needed to support the burrow, although the original burrow lining may not have been preserved. The rings may be the result of some activity unrelated to the construction of the burrow itself, such as the way the animal moved within it.

Skolithos linearis (Haldeman, 1840)

plate 11

Diagnosis

Cylindrical to subcylindrical, straight to curved, vertical to slightly inclined shafts. Shaft diameter commonly varies from 3–12 mm with lengths up to 1 metre. Shaft walls vary from distinct to indistinct and may be faintly annulated and/or lined. (after Alpert, 1974)

Occurrence

Skolithos linearis form A occurs as pipe rock in subunit 4d and as less dense shafts in subunits 2j, 2m, 2q, 3b, and 4s. *Skolithos linearis* form B was found as pipe rock in subunits 2d, 3a, and 3c, and as less dense shafts in subunits 2b, 2d, 2q, 2v, and 6d. Both pipe rock and non-pipe rock examples of forms A and B occur on float at Moraine Lake and Lake O'Hara.

Description

Specimens of *Skolithos linearis* form A consist of unlined, smooth walled, clean quartzite infilled shafts with straight tops (plate 11e). Shaft diameters vary from 5–10 mm and lengths range up to 50 cm or more. The shafts are straight overall, with local undulations that made it difficult to trace individuals over their full length in side section. Specimens are preserved as endichnia in a variety of substrates from silty shale to clean quartzite. In pipe rock, shaft separation varies from 0–5 mm. In non-pipe rock samples, the density of shafts can not be accurately determined.

Specimens of *Skolithos linearis* form B consist of smooth walled, clean quartzite infilled shafts with straight tops and dark linings less than 1 mm thick. Shaft diameters vary from 5–10 mm, lengths range up to 100 cm or more. They are straight overall with local undulations that made it difficult to trace individuals over their full length (plate 11d). Specimens are preserved as endichnia in a variety of substrates from silty shale to clean quartzite. In pipe rock, shaft separation varies from 0–10 mm with frequent overlapping of burrows (plate 11a, b). In non-pipe rock samples the density of shafts can not be accurately determined.

Discussion

Both forms conform to the diagnosis of *Skolithos linearis*. As both forms are often found together in a single bed it is probable, though not a certainty, that the absence of a lining in form A represents non-preservation of a thin lining in the original burrow. The original *Skolithos linearis* form A burrows may have had a thin mucus lining which was not visibly preserved.

The exceptionally long, pipe rock shafts in thickly bedded quartzites indicates that the optimum conditions for the trace makers coincided with periodic emergence. Overlapping burrows in the pipe rock deposits indicates that the density of burrows is greater than the density of live individuals at any one time.

Skolithos ichnosp. 1

plate 12b

=*Monocraterion* Torell, 1870

Occurrence

Skolithos ichnosp. 1 was found in subunits 2c, 5g, and on float at Moraine Lake.

Description

Specimens consist of unlined, smooth walled shafts with gently curving, funnel shaped tops and tapered lower terminations. Shaft diameter averages 5 mm and flares out to as much as 10 mm over the upper 2–10 mm of the shaft. Shaft length varies from 5–15 mm. The shafts are infilled with a dark brown, structureless quartzite.

Specimens are preserved as endichnia within amalgamated, trough cross-bedded, grey quartzites. Shafts frequently terminate at several reactivation surfaces within the beds. Vertically stacked shafts are common with vertical displacements of less than one burrow length. Densities vary from 2–6 shafts per 10 centimetres of side section. No bedding plane surfaces were observed.

Discussion

The question of the formation of shafts with funnel-shaped tops has been investigated by several authors (Hallam and Swett, 1966; Goodwin and Anderson, 1974; Crimes *et al.*, 1977; see Crimes *et al.*, 1977 for a complete discussion). The original hypothesis, that these funnels are the result of upward migration of the trace maker (Hallam and Swett, 1966) has been discarded (Crimes *et al.*, 1977). There are two currently accepted explanations for the presence of funnel topped shafts: formation by current scour (Crimes *et al.*, 1977) and formation though the activities of sessile, surface deposit-feeders in which the trace maker forms a funnel by repeatedly probing on the sediment surface around the shaft opening (Goodwin and Anderson, 1974). Goodwin and Anderson (1974) showed that funnel topped shafts occur on high tidal flats, in low energy conditions that would favour deposit-feeding more than filter-feeding. It is difficult, however, to reconcile the funnel shaped shafts in this study with the actions of surface deposit-feeding as they are preserved in amalgamated, clean, trough cross-bedded, quartzites.

The ichnotaxonomic assignment of these burrows is also a matter of debate. The contention of Goodwin and Anderson (1974) that *Skolithos* without funnel-shaped tops have had them eroded away was rejected by Crimes *et al.* (1977) who sited occurrences of straight-topped *Skolithos* in beds with gradational upper bedding surfaces. Most authors (Crimes *et al.*, 1977 for example) prefer to classify shafts with funnel shaped tops under a separate ichnogenus: *Monocraterion* Torell, 1870. Frey and Howard (1985), however, classified it as an ichnospecies of *Skolithos*. It is the opinion of the author that the latter is more appropriate approach, since both *Skolithos* and *Monocraterion* are vertical burrows, interpreted to be dwelling structures of animals that fed within a small radius of the burrow. The funnel-shaped top is either an artifact of current action or the result of a different feeding strategy. In either case the funnel-shaped top is not an integral aspect of the formation or function of the burrow.

Skolithos ichnosp. 1 differs from *Skolithos linearis* in two other aspects as well as the funnel-shaped top. The infill is consistently darker and finer grained than the host rock, the opposite of other *Skolithos* samples, and the burrow length is more than 10 times smaller relative to the diameter. These features suggest that a different trace maker, from those responsible for *S. linearis*, produced *Skolithos* ichnosp. 1. The vertical stacking of burrows indicates that the trace makers were able to readjust their burrows after deposition of thin sand layers.

Ichnogenus *Teichichnus* Seilacher, 1955

Type Ichnospecies

Teichichnus rectus Seilacher, 1955

Diagnosis

Wall shaped spreiten structures, resembling stacked U-shaped gutters, with an upper cylindrical burrow. Spreiten are almost always retrusive. Burrows are straight to slightly sinuous in plan view, rarely branched, and commonly curve upward. (after Häntzschel, 1975)

Stratigraphic Range

Teichichnus is known from the Cambrian to the Tertiary (Häntzschel, 1975).

Discussion

Teichichnus consists of long, straight, vertically stacked and overlapping burrows (Fillion and Pickerill, 1984). The basic construction and interpreted ethology are similar to that of *Phycodes* except that *Teichichnus* are longer and non-branching.

Teichichnus is interpreted to be the result of deposit-feeding from a fixed position with repeated forays down a single burrow, scraping material off the top of the burrow and packing it onto the bottom (Fillion and Pickerill, 1984; Jordan, 1985). *Phycodes* and *Teichichnus* occur in the same sedimentary facies and environments (Crimes *et al.*, 1977; Hakes, 1985; Pienkowski, 1985). *Phycodes* and *Teichichnus* sometimes intergrade however (Pickerill *et al.*, 1984), thus some trace makers must have been capable of producing both structures. In these cases, the *Phycodes* behaviour may be a response to more patchily distributed food resources.

Like *Phycodes*, *Teichichnus* represents a behaviour adapted to mining out zones of buried organic matter (Jordan, 1985), and may also be marginally adapted to exploiting dysaerobic shale layers (Jordan, 1985; see Ichnogenus *Phycodes*). It is indicative of low energy, fluctuating conditions with an abundant supply of organic material settling onto the bottom and periodic deposition sand and silt sized material. *Teichichnus* is generally formed close to the sediment surface (Fillion and Pickerill, 1984), and is generally associated with thinly bedded deposits, although exceptional examples are found on the base of thick bedded sandstones (Fillion and Pickerill, 1984).

Teichichnus has been attributed to the same animal groups as *Phycodes*: annelids and arthropods (Fillion and Pickerill, 1984), although on average, it seems to have been produced by somewhat larger animals. It is generally associated with fully marine shallow subtidal and mixed intertidal flat deposits (Fillion and Pickerill, 1984; Legg, 1985) but has been found in deposits ranging from brackish water environments (Hakes, 1985; Pienkowski, 1985), submarine fan and abyssal environments (Fillion and Pickerill, 1984), and dysoxic, interbedded sands and black shales (Jordan, 1985).

A number of other horizontal burrow and surface trail ichnogenera show *Teichichnus*-like retrusive spreiten, indicating a readjustment of the burrow position. These include *Cruziana, Gyrolithes, Ophiomorpha, Rhizocorallium, Thalassinoides* (Fillion and Pickerill, 1984), and *Trichophycus* (Osgood, 1970). *Teichichnus* can be distinguished from these ichnogenera by the presence of continuous spreiten along the length of the burrow, the lack of distinct surface ornamentation, and the lack of branching (Osgood, 1970). The term *Teichichnus* is applied only to unlined, actively infilled deposit-feeding structures (Osgood, 1970; Fillion and Pickerill, 1984).

Teichichnus rectus Seilacher, 1955
plates 14b; 15a, c, d, e, f

Diagnosis

Straight, non-branching *Teichichnus* with retrusive spreite (Fillion and Pickerill, 1984).

Occurrence

Teichichnus rectus form A was found in subunits 2b, 2j, 2l, 4x, 5d, 6e, and 6g. *Teichichnus rectus* form B was found in subunits 2j, 2m, 2o, 4n, 4r, 4s, 4t, 4w, 4x, 4y, and possibly 5d, 6a, and 6c as well as on float from Lake O'Hara. *Teichichnus rectus* form C was found in subunits 5b, 5d, 6c, 6d, and 6g as well as on float at Lake O'Hara.

Description

Specimens of *Teichichnus rectus* form A consist of less than 5 mm diameter, unlined, quartzite infilled burrows that form walls of retrusive spreite up to 10 mm deep (plate 15c, d). These walls are straight overall, although small scale lateral and vertical deflections are common. Specimens are preserved as exichnia within light brown, thinly interlaminated sandstone and shale.

Specimens of *Teichichnus rectus* form B consist of 5–10 mm diameter, unlined, quartzite infilled burrows with 1–3 retrusive spreite (plates 14b, 15f). The thickness of the spreite varies from 50–75% of the burrow diameter and are separated by thin spaces. These structures are up to 200 mm in length and are straight over their entire length.

Specimens are preserved as exichnia, and hypichnia on and near the base of thin quartzite beds, within light to dark brown shales.

Specimens of *Teichichnus rectus* form C consist of 5–20 mm diameter, unlined, quartzite to coarse sand infilled burrows with retrusive spreite. The burrow shape in parasaggital view approximates an upside-down, Log-normal frequency distribution curve: a steeply curved, concave up proximal section which curves back towards horizontal over a much broader arc (plate 15a, e). The maximum spreiten development is along the steeply curved section.

Discussion

Although the morphology of *T. rectus* form A is identical to that of the type specimen of *Teichichnus rectus* (see Crimes *et al.*, 1977) the burrow diameter is approximately one tenth that of the type material. The burrow size is similar to *Teichichnus* described by Hakes (1985) from marginal marine deposits. However, the specimens from units 2, 4, and 5 are found in ichnofossil associations indicative of fully marine conditions.

Teichichnus rectus form B is identical in both size and shape to the type material of *Teichichnus rectus* (see Crimes *et al.*, 1977). The fact that these forms are infilled with clean quartzite suggests that the trace makers fed on the sand just above the sand/mud interface where the burrows were emplaced. The thin gaps between spreiten were probably layers of fine fecal material that have weathered away. The extreme length and straightness of these forms suggests that competition for food resources was not a constraining factor for the trace makers. Such a foraging pattern would be much less efficient, compared to the compact form of *Phycodes*, in the presence of other deposit-feeding infauna (Covich, 1976). This form was usually found on the base thick quartzites which are otherwise relatively non-bioturbated and may have been below the depth at which most other deposit-feeders worked. Thus, the trace maker had no need for a spatially efficient foraging pattern.

The most distinctive feature of *Teichichnus rectus* form C is the complexly curved shape of the burrow. The steeply curved section represents the more proximal portion of the *Teichichnus* burrow extending down from the overlying quartzite bed. *Teichichnus rectus* form B and C may represent the distal and proximal portion respectively, of the same type of burrow.

Teichichnus ?stellatus Baldwin, 1977a
plates 14a; 15b

Diagnosis

A number of wall-like galleries of retrusive spreiten, radiating from a single central point to form a more or less stellar pattern (Baldwin, 1977a).

Occurrence

Teichichnus ?stellatus was found in subunits 4s and 6c.

Description

Specimens consist of a number of components, similar to *Teichichnus rectus* form B, radiating out from a central point. Although individual components are joined, there is no distinct central feature. Specimens are preserved as hypichnia on thick quartzites within grey to brown shales.

Discussion

This ichnospecies is made up of what essentially appear to be a number of *Teichichnus rectus* elements radiating from a single point (Baldwin, 1977a). There is no central feature of any sort however, (Baldwin, 1977a) which would indicate that each burrow element was an integral part of a larger structure. These structures may actually represent several *Teichichnus rectus*, formed from a common point. As most *Teichichnus rectus* are found as isolated structures, *Teichichnus stellatus* represents a unique and unusual form. However, this ichnospecies represents a group of structures, corresponding to a previously defined ichnotaxa, which are physically attached but whose formation was separated in time. As such, *Teichichnus stellatus* should not qualify as a formal ichnospecies (see Pemberton and Frey, 1982).

Ichnogenus *Trichophycus* Miller and Dyer, 1878

Type Ichnospecies

Trichophycus lanosum Miller and Dyer, 1878

Diagnosis

Large cylindrical burrows, often showing slight to marked constrictions. Burrow walls have fine striae and longitudinal ridges. Vertical branches, button-like depressions, and retrusive spreite may be present. (after Osgood, 1970; Häntzschel, 1975)

Stratigraphic Range

Trichophycus has been reported from Ordovician to late Paleozoic deposits (Häntzschel, 1975; Bergström, 1976; Seilacher, 1983).

Discussion

Trichophycus consists of cylindrical, unlined, broadly U-shaped burrows, often with irregular constrictions (Osgood, 1970). The lower surface is convex and typically covered with fine, anastomosing striae. The striae vary from longitudinal to transverse, often radiating from the centre of sections bounded by constrictions. Many generations of superimposed striae can form dense, complex patterns (see Osgood, 1970). The burrow sides and top vary from smooth to horizontally ridged and striated (Osgood, 1970). The upper surface is almost always flat or slightly concave (Osgood 1970). Burrows can exhibit curved, upward directed branches and, less commonly, sideways directed branches (Osgood, 1970). The burrow infill varies from structureless to meniscate or laminated (Osgood, 1970). Short stretches of retrusive spreiten are sometimes observed (Osgood, 1970). It is not known whether *Trichophycus* burrows were open at both ends (Osgood, 1970).

Trichophycus is interpreted as the open burrow of arthropods, probably trilobites, excavated by scratching and scraping (Osgood, 1970; Häntzschel, 1975). Its formation and general modular morphology are thought to be analogous to *Callianassa* burrows (*Thalassinoides* Ehrenberg, 1944) but without the extensive or complex burrow system of the latter. It is interpreted as a dwelling or semipermanent feeding and dwelling burrow (Osgood, 1970). The retrusive spreiten are interpreted to result from the trace maker scraping material off the ceiling and packing it onto the floor of the burrow, probably to alter the burrow configuration rather than to deposit-feeding.

Trichophycus venosum Miller, 1879

plate 16a, b, e, f

Diagnosis

Vertically branched, gently U shaped burrows in which the lower surfaces are marked by fine striae that may radiate obliquely from the lower midline (after Osgood, 1970).

Occurrence

Some specimens of *Trichophycus venosum* were found in subunits 2o, 2q, 4w, 5d, 6d, and at Moraine Lake, however, most specimens, especially the well developed ones, were found at Lake O'Hara.

Description

Specimens consist of cylindrical, unlined, clean quartzite infilled, sharp walled burrows. These are either of constant diameter or have sharp, 1–3 mm deep, constrictions spaced 10–20 mm apart (plate 16a). 5 mm diameter burrows in unit 2 have fine, transverse striae. All other burrows were 10–20 mm in diameter. Most burrows are depressed in cross-section, with the height 1–5 mm smaller than the width. These burrows have two types of ornamentation: simple, distinct, longitudinal striae; and finer, complexly anastomosing striae (plate 16b). The latter are longitudinal on cylindrical burrows and oblique to transverse on the bottom of burrows with constrictions. Burrows range from straight and horizontal (plate 16e) to broadly U-shaped (plate 16f).

Discussion

These burrows appear to have the same morphology and scratch mark patterns as Osgood's (1970) figured specimens. Except for the simple, straight morphology of these burrows, they could be assigned to *Thalassinoides*. All the burrows are quartzite infilled, within shales and mudstones. The original mud substrate must have been firm and cohesive to have supported the unlined, open burrows and preserved the fine scratch mark detail.

Trichophycus ?venosum

plate 16c, d

Occurrence

Trichophycus ?venosum was found in subunits 2j, 2o, 2p, 2q, 4s, 4t, 4u, and 5d.

Description

Specimens consist of straight, 10 mm high, 20 mm wide burrows with a laminated, alternating quartzite and thin shale infill (plate 16d). The burrow walls are covered by coarse, smooth, transverse striations and linearly arranged protrusions less than 1 mm in diameter (plate 16c). A vague lining is visible in some specimens.

Discussion

The laminated infill of these forms is probably the result of episodic, passive infill of an open burrow rather than the result of spreiten producing activities since the outline of the burrow is not effected by the laminae. These forms were assigned to *Trichophycus* since they were obviously open burrows and have distinct scratch marks. However, the scratch mark pattern does not conform to that of any known ichnospecies of *Trichophycus*.

Ichnogenus *Zoophycos* Massalongo, 1855

Type Ichnospecies

Zoophycos caputmedusae Massalongo, 1855, by subsequent designation of Andrews, 1955

Diagnosis

Variably shaped, horizontal to near horizontal, protrusive spreiten structures comprised of numerous, more or less U or J shaped burrows of variable length and orientation. The spreite are tabular or arranged in helicoid spirals giving an overall outline that is circular, elliptical, or lobate. A central, vertical tunnel or marginal tube may be present. (after Simpson, 1970; Fillion and Pickerill, 1984)

Stratigraphic Range

Zoophycos is known from Ordovician to Tertiary deposits (Fillion and Pickerill, 1984).

Discussion

The morphology, ethology, and ichnotaxonomy of *Zoophycos* has been discussed in detail by Simpson (1970) and Ksiazkiewicz (1977). The morphology of *Zoophycos* is both complex and varied. In general, it consists of a complexly shaped, often coiled sheet (lamina of Simpson, 1970) consisting of two sets of spreiten, a major set (major lamellae of Simpson, 1970) which cut across the lamina and close spaced minor lamellae which cross obliquely between major lamellae (Simpson, 1970). The degree of development of the minor lamellae varies between specimens (Simpson, 1970). The laminae range from flat or conical sheets to complex spirals, all of which vary from compact to lobate in plan view shape (Simpson, 1970). The outer edge of the lamina is made up of a burrow which is continuous at some point with an axial burrow extending towards the surface (Simpson, 1970). Extremely lobate forms of *Zoophycos* may resemble *Rhizocorallium*.

Zoophycos is interpreted as an infaunal deposit-feeding trace in which layers of organic rich sediment are systematically processed (Simpson, 1970; Chamberlain, 1977; Fillion and Pickerill, 1984). The trace maker burrows through the sediment, ingesting some components and rejecting the coarse fraction (Simpson, 1970). Rejected sediment is packed against one side of the burrow (Simpson, 1970). The burrows are repeatedly reforaged with a slight lateral offset and a layer of unprocessed sediment is packed against the rejected sediment of the previous burrow (Simpson, 1970). This alternation of sorted and unsorted sediment forms the minor lamellae (Simpson, 1970; figure 13). Ingested material is voided to the surface (Simpson, 1970). The hypothesis that *Zoophycos* represents the impression of the prostomia of sabellid worms (Plicka, 1970) is not widely accepted (FIllion and Pickerill, 1984).

Zoophycos is commonly associated with fine grained, silt to mud sized, thinly bedded, firm to stiff sediment (Ekdale *et al.*, 1984; Fillion and Pickerill, 1984; Eagar *et al.*, 1985; Miller and Knox, 1985). It is a deep deposit-feeding trace, adapted to conditions in which organic material settles out and is allowed to accumulate undisturbed at depth (Fillion and Pickerill, 1984). Thus, *Zoophycos* is indicative low sedimentation rates in settings undisturbed by waves, currents, and intense bioturbation (Fillion and Pickerill, 1984; Eagar *et al.*, 1985). For this reason, it is commonly associated with dysoxic settings (Bromley and Ekdale, 1984).

Although *Zoophycos* is most commonly associated with shallow shelf sea settings (Fillion and Pickerill, 1984; Miller and Knox, 1985), it is found in a wide variety of fully marine settings from back barrier lagoons and intertidal flat siltstones (Miller and Knox, 1985) to deep basin black shales (Jordan, 1985). *Zoophycos* has been attributed to the activities of annelids and sipunculids (Simpson, 1970; Fillion and Pickerill, 1984).

?*Zoophycos*
plate 10c

Occurrence

?*Zoophycos* was found in subunits 6a, 6c, and 6e.

Description

Specimens consist of vague spreiten-like swirls within silty, fine sandstone or siltstone. They form 20–45 mm wide strips of fine, 1–3 mm wide, slightly curved spreite. There are never any indications of marginal burrows. The length of the strips varies from 40–500 mm. There was one instance where a natural distal termination was seen but no terminal burrow was evident.

Discussion

These structures are oriented parallel to the trend of undulations in the sediment so that it is unlikely that they are physical sedimentary structures. They are preserved in sparsely bioturbated, thinly bedded siltstones and shales which is the common sedimentary setting of *Zoophycos*.

The strip-like form of these structures bears a superficial resemblance to both *Zoophycos* and *Rhizocorallium* Zenker, 1836. *Zoophycos* and the long strip-like forms of *Rhizocorallium* are both thought to be the result of systematic deposit-feeding in a distinct horizon. Thus, there would be no appreciable affect on the ethological or environmental interpretation if the structures in this study have been misidentified either way.

DESCRIPTIVE AND INTERPRETIVE SEDIMENTOLOGY

Redoubt Mountain Section

The Gog Group at Redoubt Mountain can be divided into 7 informal stratigraphic units (Palonen, 1976; plate 1a, b; figures 14–22). These alternate between resistant, cliff forming units dominated by thick, cross-bedded quartzites and recessive units made up of interbedded quartzites, siltstones, and shales (figure 15). The informal units used in this study closely approximate those of Palonen (1976). The only exception is that the boundary between units 4 and 5 which was moved up approximately 35 m in this study, to coincide with the base of the third interval of cliff forming quartzites. Unit 7 was not investigated due to lack of time and bad weather.

No extensive environmental reinterpretations are made in this study, especially where physical sedimentary features are concerned. Environmental interpretations made herein draw heavily upon the paleoenvironmental summaries of Palonen (1976) and Young (1979). A summary of the paleoenvironmental and paleogeographic reconstruction for the Gog Group is given in Chapter 1 (figure 16). The primary purpose of this chapter is to place the trace fossils into an existing sedimentary and paleoenvironmental framework.

A stress is placed on physical sedimentary features for environmental interpretation in this study, rather than on the biogenic structures. The reason for this is that, while strict uniformitarianism can be applied to physical processes, its value with regards to biological, (especially ecological) processes decreases with increasing geologic antiquity. A good example of the differences in lower Paleozoic ecological patterns is the occurrence of graphoglyptid burrows in Lower Cambrian shoreface and offshore deposits, while they are largely restricted to deep ocean deposits throughout the rest of the Paleozoic (Crimes, 1974; Crimes and Anderson, 1985).

Unit One Description

Unit 1 consists of a 55.5 m thick cliff of cross-bedded, fine-grained quartzite beds (Palonen, 1976; figure 17) with intercalated grey to black shale which could only be observed as thin flakes adhering to the bottom surfaces of the quartzite beds. Unit one can be divided up into four zones, based on bedding style, sedimentary structures, and the granulometric properties of the quartzite (Palonen, 1976).

Zone 1 comprises the basal bed of the unit. It overlies a major regional unconformity, separating it from the underlying Miette Group slates (Aitken, 1969; Palonen, 1976; plate 1c). It consists of a 1 m thick, tabular bedded, clean, fine grained, conglomeratic, quartzite. No ichnofossils or physical sedimentary structures were found in this zone.

Zone 2 consists of 10–15 m of 10–100 cm thick, tabular bedded, flat laminated to low angle cross-stratified, fine grained quartzite with occasional intercalations of grey shale, less than 5 mm thick. Two distinct types of mud cracks occur sporadically on otherwise smooth basal surfaces: those with ridges having angular cross-sections and those with U-shaped to semicircular cross-sections. The former consists of 10 mm wide, 5 mm relief ridges forming irregular hexagonal cells 12–15 cm across (plate 3a, d, f). The latter consists of 50 mm wide, 10 mm relief ridges forming irregular, polygonal cells 10–12 cm across (plate 3c). The relief of these structures indicates that the original thickness of shale intercalations must have been at least 10 mm. Both variants are likely the result of desiccation rather than subaqueous shrinkage as the later tends to form cracks with irregular radiating and crosscutting patterns rather than polygonal cells (Collinson and Thompson, 1982). The tabular beds are occasionally interrupted by 25–100 cm thick lenticular beds consisting of a basal planar cross-bed set and upper amalgamated trough cross-bedding. Few biogenic structures occur in this zone; the only distinct structure found was a 3 mm diameter, horizontal burrow, resembling *Planolites montanus*, situated on the base of a thin quartzite bed.

The boundary between zone 2 and zone 3 is gradational over at least 5 metres of section. Zone 3 comprises the remainder of unit 1, with the exception of a variable number of beds (usually less than 5) occurring at the top of the unit. It is characterised by lenticular quartzite beds, similar to those in zone 2, and tabular bedded quartzite composed of single planar cross sets. These two bedding styles are mixed throughout the zone, although each was noted to predominate in certain areas and at certain stratigraphic levels along the outcrop. Herringbone cross-stratification is commonly developed. Although there are some beds with irregularly mottled basal surfaces, no distinct biogenic structures were found except for the top 4 m of section which contains occasional 5 mm diameter *Skolithos linearis* form A.

Zone 4 makes up the upper few beds of unit 1. It consists of tabular quartzite beds, up to 50 cm thick, completely burrowed with 5 mm diameter, *Skolithos linearis* form A, which extend completely through the beds. The average separation between adjacent shafts is 1–2 mm, resulting in a pipe rock structure (*sensu* Hallam and Swett, 1966). No physical sedimentary structures were evident. There are also occasional 7 mm diameter *Skolithos linearis* form B, with thin black linings, making up less than 5% of the total number of shafts. Both forms of *Skolithos* are infilled with quartzite that is slightly lighter in colour than the host rock.

Unit One Interpretation

Palonen (1976) interpreted unit 1 to have been deposited in a narrow, high energy shelf sea and found no evidence for fluvial processes in the Lake Louise area. It represents the initial progradational influx of sediments derived from the uplift on the craton margin (Young, 1979) and is then followed by a major transgression recorded by the occurrence of *Skolithos* near the top of the unit 1 and the interbedded shale and quartzite of unit 2 (Palonen, 1976). The decreasing prominence of swash deposits, and the concomitant increase of tidally produced features up section is perhaps indicative of an increase in shelf width and a relative rise in sea level (Palonen, 1976).

Zone 2 has been interpreted as having been deposited in a swash zone setting, such as the backshore to foreshore environment of Elliott (1986). Flat laminated and low angle cross-bedded tabular quartzites with sharp, flat bedding planes and sparse to absent bioturbation are all diagnostic features of this environmental setting (Palonen, 1976; Baldwin, 1977a; Elliott, 1986). The desiccation cracks are likely the result of the drying up of tide pools between the higher tidal cycles (Goodwin and Anderson, 1974; Palonen, 1976). These pools may have been periodically inhabited by burrowing organisms as evidenced by the sporadic occurrence of *Planolites*.

Zone 3 has been interpreted to be a combination of tidal flat and subtidal channel deposits (Palonen, 1976). The lenticular quartzite beds and herringbone cross-stratification are the result of sand bars migrating across an intertidal flat (Palonen, 1976; Collinson and Thompson, 1982, figure 6.26). The interbedded, tabular bedded quartzites were deposited in shallow, migrating tidal channels (see Goodwin and Anderson, 1974; Palonen, 1976). Deposits in which tabular planar cross-stratified beds predominate probably reflect deposition in larger subtidal channels (see Goodwin and Anderson, 1974; Palonen, 1976). The thin shale interbeds and occasional bioturbate texture on some basal surfaces may be the result of standing water in tidal ponds and low areas within tidal channels between the higher tidal cycles (Goodwin and Anderson, 1974).

The sole visible difference between zones 3 and 4 is the conspicuous presence of *Skolithos* pipe rock in the latter. The emplacement of *Skolithos* is most likely related to some combination of increased sediment stability and duration of submergence in each tidal cycle (Goodwin and Anderson, 1974). The dense packing of tubes, which may be higher than the actual density of live animals at any one time (see Ichnogenus *Skolithos*), indicates optimum conditions of submergence and suspended food supply (Goodwin and Anderson, 1974). The extreme depth of the shafts is indicative of periodic emergence (Goodwin and Anderson, 1974) indicating that this deposit was still within the intertidal zone. The tabular bedding style suggests that this zone was deposited along the sides of deep tidal channels, similar to the deposits of zone 3, but probably closer to the mean low water mark. Occasional *Skolithos* near the top of zone 3 implies a gradual transgression from zones 3 into zone 4. Zone 4 comprises a transitional environment between the the tidal flat deposits of unit 1 and the shallow subtidal deposits of unit 2 above.

Unit Two Description

There is a sharp transition between units 1 and 2, with the upper most thick pipe rock bed of unit 1 directly overlain by thin, tabular bedded quartzites and black shales of lower unit 2. Unit 2 is composed of alternating intervals of thick quartzite beds and intervals of interbedded wavy bedded shale and thin quartzites (figures 15, 18, plate 1d). Based on the bedding style of the quartzite beds in unit 2, two zones can be recognised.

Zone 1

Zone 1 forms the basal 25.5 m of unit 2, comprising subunits 2a to 2f (figure 18). It is characterised by regular, tabular bedded quartzites which generally show no internal structure although some exhibit vague mottling or amalgamated cross-bedding. The dominant feature of this zone are 10–50 cm thick, tabular bedded, fine to medium grained, quartzites. These are interbedded with 1–150 cm thick intervals of dark, thinly fissile shale and wavy bedded shale and 1–15 mm thick quartzite stringers (plate 2c). Thin quartzite beds (5–15 cm thick) are common in the thicker shale intervals; occurring as isolated beds and clusters of up to ten beds separated by thin shale partings. Bedding plane exposures were difficult to obtain due to the abundance of thick, well indurated quartzite beds. Thus, the distribution of ichnofossils on bedding plane surfaces could only be roughly estimated from rather sporadic finds.

Biogenic structures are very rare within the shales, limited to occasional *Planolites montanus* and quartzite infilled *Palaeophycus* ichnosp. A more diverse ichnofossil assemblage occurs on the basal surfaces of quartzite beds and within the thinner quartzite beds and quartzite stringers. Trace fossils occur as discrete forms rather than dense, interpenetrating burrows; no obvious cross-cutting relationships were observed. The most abundant forms are *Planolites montanus*, *Chondrites* form D, *Palaeophycus tubularis*, *P.* ichnosp., and *Phycodes palmatum* form A. Surface trails and excavations, including *Bergaueria perata*, *B.* ichnosp., *Diplichnites* form A, *Rusophycus* ichnosp. 3, and *R. rugosa* occur sporadically on the base of thin quartzite beds. There is little overburrowing of the surface trace fossils by either simple burrows (e.g *Planolites*) or complex deposit-feeding structures (e.g. *Phycodes*). Other ichnofossils are present in minor amounts in this sequence: *Arenicolites* ichnosp. on the upper surfaces of thin quartzites and *Chondrites* form A, *Phycodes circinatum*, *Teichichnus rectus* form A, and *Trichophycus* on the basal surfaces of thin quartzites. The most intense bioturbation occurs in the shale partings within the clusters of thin quartzite beds; consisting primarily of tortuous and interpenetrating *Planolites montanus*, with minor occurrences of *Palaeophycus* ichnosp. and *Phycodes* ichnosp. *Diplichnites* form B, *Rusophycus parallelum*, and *R. bilobatum* form locally dense assemblages on the basal surfaces of thick quartzite beds. The basal surfaces of the thick quartzites show almost no post depositional biogenic structures.

Approximately half of the thick quartzite beds contain *Skolithos linearis* form B: 4–6 mm diameter shafts with thin, black linings and light coloured quartzite infills. In most cases, the shafts are well dispersed, however, small number of beds contain dense clusters of 5–20 shafts with inter-shaft separations as low as 2 mm and separations between clusters ranging from 5–20 cm (plate 11f). One thick quartzite bed contains a number of unlined, funnel shaped *Skolithos* ichnosp. 1. These shafts have upper terminations at at least three levels within the quartzite bed, indicating the presence of several reactivation surfaces.

Zone 2

Zone 2 comprises the rest of unit 2 and is characterised by lenticular bedded quartzites. Deposits alternate between intervals of thick quartzite beds with thin shaly interbeds and intervals dominated by wavy bedded shale and quartzite laminae with thin quartzite beds (figure 18).

The shaly intervals vary from 1.5–15 m thick with a mode of approximately 5–7 m. They consist of smaller, 1–5 m thick, sequences of wavy bedded shale and quartzite laminae capped by a dense cluster of thin quartzite beds, up to 50 cm thick in total. Thin quartzite beds occur within the shales and increase in thickness and frequency up section from the base of the sequence to the base of the quartzite bed clusters, forming small coarsening upward sequences (plate 1d). These coarsening upward sequences grade into, and are capped by clusters of quartzite beds separated by wavy bedded shales, less than 1 cm thick.

The base of some of the smaller sequences is made up of linsen bedded dark shale and 5–10 mm thick quartzite lentils making up less than 50% of the rock volume (plate 2c). Interspersed with this are 1–10 cm thick quartzite beds making up 5–15% of the rock volume. These beds are continuous, but irregular in thickness with undulatory upper surfaces. Linsen bedded shales contain few ichnofossils, mostly horizontal to subhorizontal burrows: *Chondrites* forms B and D, *Palaeophycus tubularis*, and *Planolites montanus*. Complex feeding traces, such as *Phycodes palmatum* and *Teichichnus rectus*, and surface emplaced traces, such as *Rusophycus* and *Bergaueria*, are extremely rare. Burrows were seen within and on the surfaces of the quartzite lentils, often forming dense intertwining patterns of distinct burrows; surfaces that are bioturbated to the point of being indistinctly mottled were not found.

The bulk of the individual coarsening upward sequences is made up of wavy bedded dark shale and thin quartzite laminae, interspersed with 1–20 cm thick quartzite beds (plate

2a, c). There are few recognisable physical sedimentary structures within either the quartzite beds or laminae. The spacing between the quartzite beds is irregular, varying from 1–100 cm, but generally decreases up section within the sequences, from an average of 15–25 cm to less than 1 cm within the quartzite bed clusters capping the sequences. Near the top of the sequences, the thin quartzite beds are often formed of tight clusters separated by thin, black shale partings. The parting planes are usually intensely bioturbated with intertwining and interpenetrating horizontal burrows, while the quartzite beds are internally mottled. Upper bedding surfaces are smooth and undulatory. Interference ripples and symmetrical ripples with planed off crests are common on the upper surfaces of the quartzite laminae, and thin quartzite beds, in coarsening upward sequences near the top of unit 2 (plate 4c, d, f). Lower bedding surfaces vary from smooth to densely bioturbated; small load casts are locally abundant but rare overall. The basal surfaces show casts of horizontal burrows and complex feeding traces which often extended through the laminae. Synaeresis cracks are locally abundant. Irregular basal surfaces, consisting of oval to circular pits, were seen on a few of the thicker quartzite beds within the quartzite bed clusters near the top of unit 2 (plate 5f).

The shaly intervals contain dense and diverse ichnofossil assemblages. Both the diversity and density of ichnofossils increase up section in the smaller sequences along with the increasing frequency of quartzite beds. The basal wavy bedded shales and quartzites are dominated by simple burrows, *Palaeophycus tubularis*, *P. striatus*, and *Planolites montanus* as well as *Chondrites* forms A and D, all of which occur as distinct structures along the surface of quartzite laminae. *Rusophycus* ichnosp. occurs very rarely as discrete quartzite infilled casts within the wavy bedded shale and quartzite laminae (plate 2f). *Trichophycus ?venosum* occurs sporadically as isolated burrows throughout these sequences (plate 16d).

Bioturbation becomes more pervasive up section with the increase in thickness and frequency of thin quartzite beds, peaking just below the quartzite bed clusters at the top of the coarsening upward sequences with multiple generations of overburrowing and interpenetration. *Phycodes palmatum* form A, *P.* ichnosp., and *Teichichnus rectus* form A are common along the base of thin to medium quartzite beds, throughout the coarsening upward sequences. *Bergaueria perata* and *Rusophycus rugosa* occur rarely on the basal surfaces of thin quartzite beds towards the top of the coarsening upward sequences. Surface emplaced trace fossils are most common just below the quartzite bed clusters. These include *Diplichnites* forms A, B, and C, *Monomorphichnus* form B, *Cruziana goldfussi*, *C. plicata*, *C. semiplicata* form A, *C.* ichnosp. 4, *Rusophycus avalonensis* forms A and B, and *Rusophycus bilobatum* forms A and B. Basal surfaces of many of the thinner quartzites are intensely bioturbated by *Chondrites*, *Palaeophycus*, *Phycodes*, *Teichichnus* and *Planolites*, all of which over-burrow the surface emplaced trace fossils. Post depositional biogenic structures are concentrated on and just below the quartzite lower bedding surfaces. The basal bedding surfaces of the thicker quartzite beds are only sparsely bioturbated with respect to post depositional trace fossils, although *Chondrites* form A and *Gordia marina* are locally abundant on otherwise smooth, non-bioturbated surfaces (plates 8f, 10d). *Skolithos linearis* occurs sporadically as isolated shafts within both the bioturbated and non bioturbated thin quartzite beds, and more frequently as patches of densely packed shafts within the quartzite bed clusters.

The shaly intervals are capped by 1–6 m thick intervals of 10–50 cm thick lenticularly bedded, fine grained, trough cross-bedded quartzite and thin shaly interbeds (figure 18, upper right of plate 1d). Basal surfaces are sharp with sporadic *Planolites montanus*, *Gordia marina*, and *Chondrites* form D, along with infrequent *Chondrites* form A, *Phycodes*, and poorly preserved *Rusophycus*. Upper bedding surfaces are smooth and broadly undulatory. The shaly interbeds were difficult to sample due to their thinness and recessive nature.

Interspersed within unit 2 are 40–500 cm thick intervals of 25–150 cm thick quartzite beds with thin shale interbeds (subunits 2c, h, m, and p in figure 18). The quartzite beds vary from coarse grained and mottled throughout to massive, poorly sorted, coarse, conglomeratic quartzite that fines up through medium grained, flat to low angle laminated quartzite, to fine-grained, trough cross-bedded quartzite. Lower bedding surfaces are sharp and irregular, upper bedding surfaces are smooth and broadly undulatory. The quartzite beds contain no ichnofossils. The interbedded shales consist of 1–10 cm thick, linsen to wavy bedded dark shale with occasional *Planolites* ichnosp. and vague *Rusophycus* ichnosp. on the base of the thinner quartzite beds.

Unit Two Interpretation

Unit 2 is dominated by upward coarsening sequences in which quartzite beds become both thicker and more frequent up section at the expense of the intercalated shales, culminating in a cap of thick quartzite beds with thin shale intercalations and parting planes. The base of each sequence is formed by the sharp contact of shale beds over the thick quartzites of the lower sequence. Palonen (1976) concluded that coarsening upward sequences are the result of abandonment and infilling of tidal channels. The sudden change from quartzite to shale at the top of each sequence is compatible with a sudden termination of sediment supply. Continued buildup of muddy sediment in each sequence, raising the sediment surface through increasingly higher water energy regimes, is thought to have resulted in the coarsening upward sequences. The sequences appear to be locally developed over areas of less than 1 square kilometre (Palonen, 1976). The sequences are not thought to represent sea level fluctuations because of their large number; the increasing number from east to west into deeper water deposits; their lateral discontinuity; and the wide variation in thickness between sequences with the same relative thickness of each sediment type. They are too thick to have resulted from migrating sand bars. The intervals of very thick quartzite beds probably resulted from storm activity, sediment slumps, or other catastrophic events.

Unit 2 is the culmination of the deepening upward trend seen in unit 1. The continuity of the first recessive unit over a wide area of the Cordillera indicates deposition during a major marine transgression (Palonen, 1976). The predominance of wavy, flaser, and lenticular bedded quartzites and shales with abundant thin quartzite beds suggests a lower intertidal to shallow subtidal (upper offshore of Elliott, 1986) environment with a high frequency of fluctuations between quiet water and energetic conditions (Reineck and Singh, 1975; Palonen, 1976; Elliott, 1986). This is supported by the close association of infaunal and surface deposit-feeding trace fossils, such as *Planolites* and *Cruziana*, and filter-feeding trace fossils, such as *Skolithos*. A gradual shallowing upward trend occurs in the upper part of the unit, as shown by the presence of interference ripples and planed off ripples on the upper surface of thin quartzite beds and lentils (plate 4c, d).

The coarsening upward sequences contain mostly simple horizontal burrows in the wavy bedded shales with an increasing abundance of surface trace fossils and complex deposit-feeding traces up section as the proportion and thickness of quartzite beds increases. The rarity of surface emplaced trace fossils, such as *Cruziana* and *Bergaueria*, in the wavy bedded shales and quartzites near the bottom of the coarsening upward sequences is probably a result of poor preservation after emplacement. The rate of sedimentation resulting in these deposits was probably not great enough to bury surface traces before they were reworked by physical and biogenic processes. Rare occurrences of these structures in the wavy bedded shales shows that they were produced in these settings (plate 2f).

The increase in frequency of complex deposit feeding traces such as *Teichichnus*, *Phycodes*, and *Chondrites*, however, probably represents a real environmental preference on the part of the trace makers. These traces are produced through the utilisation of deep buried concentrations of organic detritus and thus, would only be produced below thick beds that were deposited quickly, concentrating surface detritus and dead animals in a thin horizon. Organic detritus is probably too diffusely distributed in the wavy bedded shales to support this type of deposit-feeding.

Surface trace fossils are often extensively over-burrowed by horizontal deposit feeding traces, such as *Planolites* (plate 26a). Simple deposit-feeding burrows, such as *Planolites*, are also concentrated along the base of thin and medium sand layers. Basal bedding surfaces of very thick quartzites (greater than or equal to 20 cm thick) show very little evidence of post depositional biogenic reworking, although they may preserve abundant surface trace fossils and the shales below contain abundant horizontal and complex deposit-feeding trace fossils. This suggests that most of the infaunal deposit-feeding animals were unable to penetrate this deep into the sediment, either because of mechanical constraints on their digging ability or from the development of dysoxic conditions at depth. Some of these bedding surfaces, however, are covered with monotaxonomic assemblages of either *Chondrites* or *Gordia*. The *Chondrites* behaviour is specifically adapted to the utilisation of deeply buried material.

Skolithos shafts are common in the thicker quartzite beds reflecting the presence of higher energy conditions, suitable for filter-feeding, and the absence intense deposit-feeding. The presence of *Skolithos* in the wavy bedded shales is probably not related to the environment of the wavy bedded shales themselves. These shafts were probably emplaced in thin surface sand layers and extended down into interbedded sand and mud which was no longer being actively bioturbated (S. Vossler, pers. comm., 1988).

The wavy bedded shale and quartzite in the upper shaly intervals shows evidence, in the form of interference and planed off ripples, for having been deposited in very shallow to emergent conditions. These deposits still contain abundant surface trace fossils such as *Rusophycus* (plate 4d, f). This indicates that trilobites and other epifauna were active in the lower intertidal zones. The deep *Rusophycus* in plate 4f may have been dug to escape exposure or high currents associated with the tidal cycle.

Unit Three Description

Unit 3 consists of a single, 61 m thick sequence grading up section from thick flaser bedded pipe rock and interbedded shale and quartzite to thickly bedded, massive orthoquartzites (figures 15, 16, 19). The lowest thick pipe rock bed forms a convenient marker for the base of unit three, however, the transition from unit 2 to unit 3 is actually gradational over several metres of section.

The basal 16 m of the unit consist of 1–3 m thick intervals of 25–150 cm thick, lenticular, brown to grey coloured quartzite beds and 10–100 cm thick intervals of interbedded 1–20 cm thick quartzite beds and wavy bedded shale and quartzite laminae. The shaly intervals are thickest and most frequent near the base of this zone. The lower shaly interval contains numerous large (greater than 10 cm across), poorly preserved ***Rusophycus bilobatum*** form B on the base of the quartzite beds. These are densely overburrowed with ***Planolites montanus*** and ?***Palaeophycus*** which, along with ***Phycodes***, are also found in the shale and quartzite laminae. The upper shaly intervals contain only occasional ***Planolites montanus***. ***Skolithos linearis*** extend through the wavy bedded shales from the quartzite beds.

Approximately 75% of the thick quartzite beds, within both the quartzite and shaly intervals, are made up of flaser bedded *Skolithos* form B pipe rock (*sensu* Hallam and Swett, 1966; plate 11a, b, d)). The *Skolithos* are 5–9 mm in diameter with a white quartzite infill and a 0.5 mm thick, dark lining. Shafts are straight to locally undulating (plate 11d) and pass through the entire thickness of the beds, over 1 metre in some cases. In the lower beds, shaft separations are less than 1 mm, with occasional overlapping shafts. The density of shafts decreases up section to approximately half this density at the top of the zone. The other 25% of the quartzite beds are made up of clean quartzite, approximately half of which contain well spaced (1–10 cm) *Skolithos* shafts. No physical sedimentary structures were observed in any of the quartzite beds.

This zone is overlain by 32 m of 10–50 cm thick, lenticular, clean white and flaser bedded quartzite beds. These alternate between 3–6 m thick zones of massive quartzite and zones of trough cross-bedded quartzite. *Skolithos* is present in decreasing density up section, disappearing completely above the 22 m mark. Occasional *Planolites*-like burrows are seen on basal surfaces in the lower 9 m. *Skolithos* occurs in both the cross-bedded and flaser bedded quartzite. The upper-most 12 m of unit 3 consists of two 2–3 m thick beds of white, massive quartzite overlain by 7 m of 10–75 cm thick, massive, lenticular quartzite beds. Weathered surfaces are white, with a porcellaneous texture.

Unit Three Interpretation

Unit three is the culmination of the shallowing upward trend that starts near the top of unit 2. Palonen (1976) interpreted this regressive trend as the result of sedimentary progradation. It passes through three depositional environments.

The lowest zone was deposited in a setting similar to the lower tidal flat environment of zone 4, unit 1. The exceptionally deep *Skolithos* tubes indicate that this area was subject to periodic, prolonged emergence. The high density of shafts, however, suggests that conditions for filter-feeding were still close to optimum. The overlapping of shafts indicate the presence of several generations of shafts, and that the shaft linings were not especially cohesive. These quartzite beds were probably along the edge of large, stable tidal channels, within the intertidal zone. The shaly intervals may have resulted from periods of channel abandonment. The large *Rusophycus* found in these intervals indicates the presence of large trilobites, which were obviously able to survive in this higher energy regime. They may have preyed upon stationary infauna, such as the *Skolithos*-makers.

The middle zone was deposited on a high energy, sand dominated intertidal flat (Palonen, 1976). The decreasing density of *Skolithos* up section indicates a steady decrease in sediment stability and duration of submergence as the area shifted from a lower to upper tidal flat setting.

The upper thick to very thick quartzite beds contain no physical or biogenic sedimentary structures that might potentially yield clues as to the environment of deposition. Young (1979) postulated that these deposits might have been deposited in a foreshore–shoreface environment which was later elevated to a backshore setting with continued regression. The lack of internal structure could be due to micro-scale slumping caused by the downward movement of meteoric water (Young, 1979). The extremely clean, well sorted nature of the quartzite is consistent with a beach interpretation.

Unit Four Description

Unit 4 is divided into 3 distinct zones: a lower zone dominated by poorly indurated sandstone and green and red mudstone; a middle zone dominated by thin, flat to low angle cross-stratified, poorly indurated sandstone; and an upper zone dominated by lenticular bedded, well indurated quartzite and wavy bedded shales, similar to unit 2 (figures 14, 16, 20).

Zone One

This zone comprises subunits 4a to 4h, and is made up of a number of different intervals. The basal metre of section consists of 20–40 cm thick beds of pale green, soft, coarse sandstone with a mottled, possibly bioturbated texture. This interval contains few discrete, though vaguely defined, ichnofossils (*Diplocraterion* ichnosp., *Planolites montanus*, and *Skolithos linearis* form A). This grades, within the upper-most bed, into a 1 m thick bed of well indurated, fine grained, pink, apparently massive quartzite (plate 2e), containing abundant *Arenicolites* ichnosp. and *Skolithos linearis*, both averaging 15 cm in depth. The shafts have weathered out peripheral gaps suggesting that the shafts were originally lined. The *Arenicolites* averages 15 mm in width between the arms, giving depth to width ratios of 10–30. Although true upper terminations could not be identified, the shafts seemed to terminate at several levels near the top of the bed.

The remaining 8 m of section consists of alternating sequences of bedded sandstone and soft, sandy, red and green mudstone with frequent layers of coarse sand and pebbles a few grains thick. Colour patches do not coincide with bedding or any other sedimentary feature. The sandstone is poorly indurated and poorly sorted, with a decrease in grain size decreases up section and a concomitant increase in sorting. Few physical sedimentary structures can be seen and most beds have a mottled structure. The sandstone beds occur in clusters with intercalated mudstone and less frequently as individual thin beds. The thickness and frequency of both the clusters and individual beds decreases up section. Synaeresis cracks and desiccation cracks are common on upper bedding surfaces of thin sandstones, especially near the top of the interval.

Skolithos linearis form B is abundant throughout the thick, mottled and flaser-bedded sandstone, ranging from a pipe rock at the base of the interval (plate 11c) to rare individual shafts within the thin sandstone beds at the top. A 2–5 mm diameter shaft occurs throughout the interval, while a 7–11 mm diameter shaft is interspersed with the smaller diameter shafts in the lower 2 to 3 clusters. Both types of *Skolithos* exhibit 2–3 cm long undulations making it difficult to follow the burrows in side section. The maximum recorded length was 12 cm.

The only abundant trace fossil in the mudstones is *Planolites montanus*, along with very rare shallow *Diplocraterion, Diplichnites* form D, *Monomorphichnus* ichnosp., *Phycodes palmatum* form A, *P. flabellum*, and *Rusophycus bilobatum*.

Zone Two

Zone 2, comprising subunits 4j to 4k, consists of 19 m of alternating 2–6 m thick intervals of 5–30 cm thick, poorly indurated, flat laminated to low angle cross-stratified sandstones with thin shale partings, and intervals of wavy bedded shale, siltstone, and sandstone stringers with 1–5 cm thick sandstone beds making up less than 25% of the volume. The sandstone beds split along horizontal, flat parting planes with no evidence of lithologic discontinuities. There is no evidence of internal bioturbation however, roughly 25% of the lower bedding surfaces show casts of profuse but largely unidentifiable bioturbation. Some trace fossils were tentatively identified as *Monomorphichnus* and *Phycodes*, and *Planolites*. Run-off marks, mud cracks, wind adhesion ripples, interference ripples, and small load casts are common on sandstone bedding surfaces throughout this zone (plate 4). No distinct biogenic structures were seen within the shales and siltstones.

Zone Three

Zone 3 comprises the rest of unit 4, and consists of alternating recessive and resistant intervals of lenticular bedded quartzite and wavy bedded shale and quartzite stringers. This zone is similar to unit 2, zone 2 except that the shales are lighter in colour and weather to a strong orange colour. As well, there are no obvious coarsening upward cycles. The resistant and recessive intervals can be divided into three general types.

Type one consists of medium to thick and tabular to lenticular bedded, fine grained, reddish brown to grey quartzites with thin interbeds of grey to dark grey shale and wavy bedded shale and quartzite. The quartzites are predominantly trough cross-bedded although occasional beds of planar cross-bedding occur. Basal surfaces are sharp, often with coarse lags, and vary from flat to irregular on a centimetre scale. Groove marks and other tool marks are occasionally found. Upper bedding surfaces are sharp, smooth, and often broadly undulatory. Observation of the shaly interbeds were difficult to make due to their thinness and recessive nature. These intervals have ichnofossil assemblages ranging from barren to extremely diverse, although even the barren zones had mottled basal bedding surfaces suggestive of bioturbation. This range of diversity and density is apparently due, at least in part, to preservational effects: the ability to observe the shale interbeds and the lower quartzite bedding surfaces and the grain size and sorting of the lower quartzite bedding surfaces. In the most diverse zones, the basal surfaces of the quartzite beds, as well as the interbedded wavy shales, contained assemblages similar to interval type two (see below). *Skolithos* occurs sporadically within the quartzite beds.

Type two consists of thin to medium, lenticular bedded, fine-grained, trough cross-bedded quartzites. Lower surfaces are sharp, fine grained, and show well preserved ichnofossils as well as abundant groove marks, bounce marks, and chevrons. A common form of groove mark towards the top of unit 4 consists of 5–100 mm long, strait to slightly curving, hair-like ridges, less than 1 mm wide (see plate 5d). Upper surfaces are commonly composed of lunate dune bed-forms (plate 3e). Quartzites are interbedded with thin layers of wavy bedded shale and quartzite.

The lower surfaces of thin quartzite beds and quartzite stringers in the wavy bedded shales show isolated *Cruziana stromnessa, Diplichnites* forms A, B, and D, *Monomorphichnus* forms A and B, *Palaeophycus striatus, Phycodes palmatum, Planolites montanus, Protichnites* ichnosp., *Rusophycus eutendorfensis* form C (plate 27a, b), and *Trichophycus ?venosum.*

The undersurfaces of 5–30 cm thick quartzite beds show extremely dense bioturbation with a wide variety of behavioural types represented, including: *?Arenicolites, Bergaueria hemispherica, B. perata Chondrites* forms A, B, and C, *Cochlichnus* ichnosp., *Cruziana C. plicata, C. semiplicata* form B, *C. stromnessa, C.* ichnosp. 4, *C.* ichnosp. 2, *Didymaulichnus lyelli, Diplichnites* forms A, C, and D, *Diplocraterion* ichnosp., *Monomorphichnus* forms A and B, *Palaeophycus striatus, P. tubularis, Phycodes flabellum, P. palmatum* forms A and B, *Planolites annularis, P. beverleyensis, P. montanus Protichnites* ichnosp., *Rusophycus bilobatum, R. carinatus, R. eutendorfensis, R.* ichnosp. 3, *R.* ichnosp. 2, *Skolithos linearis* form A, *Teichichnus rectus* forms A and B, *T. ?stellatus, Trichophycus venosum, T. ?venosum*, and *?Trichophycus.*

Many lower bedding surfaces consist of dense ichnofossil associations in which the surface traces, *Bergaueria, Cruziana*, and *Rusophycus*, are overburrowed by a wide variety of horizontal burrows and complex feeding traces. The diversity of ichnogenera on these lower bedding surfaces often approximates that of the zone as a whole. These surfaces are similar to the densely bioturbated surfaces of unit 2 with random orientation and spatial association of horizontal burrows and a number of generations of overburrowing and interpenetration.

Several other ichnofossil associations occur in these intervals. *Didymaulichnus lyelli* often occurs as dense looping and overlapping trails, in the absence of most other ichnofossils, on the base of medium quartzite beds (plate 20a–d). Other lower bedding surfaces show dense assemblages of short *Cruziana* ichnosp. 1 and *Rusophycus* ichnosp. 3, forming overlapping and serially arranged trails and pits, along with sporadic *Teichichnus rectus* form B and *Teichichnus ?stellatus* (plate 21a). Dense clusters of *Bergaueria hemispherica* and *?Dolopichnus* are also common on the base of medium quartzite beds, with inter-burrow spacing in the range of 0–10 mm. *Cruziana clavata*, *C. pormensis*, and *Teichichnus rectus* form B occur as isolated, quartzite filled structures in shale, just below quartzite beds. *Gordia marina* occurs on the basal surfaces of thick, non-bioturbated quartzite beds. *Skolithos linearis* form A occurs sporadically throughout the quartzite beds.

The basal interval of zone 3 is of this type, although it also contains several tabular to slightly lenticular beds of coarse, well indurated, purple to white quartzite. These beds vary from trough cross-bedded to planar cross-bedded and massive in the thicker examples.

Interval type three is similar to type two except the wavy bedded shales make up 30–70% of the rock volume. The quartzite beds are predominantly grouped into clusters although very thin quartzite beds are found throughout the shales. Both the quartzite beds and wavy shale zones were ichnofossiliferous, and although the overall diversity and range of ichnological associations is identical to interval type 2, the diversity of forms on individual bedding surfaces is much lower. Horizontal burrows and complex feeding structures predominate over surface trails and excavations.

Unit Four Interpretation

Zone 1 of unit 4 has been interpreted as having been deposited in a restricted, periodically hypersaline lagoon (Palonen, 1976). Desiccation cracks and oscillation ripples are common, indicating periodic shallow water and emergence. Synaeresis cracks are also seen indicating fluctuations in salinity. Palonen (1976) noted the presence of cubic depressions in shales, indicating the presence of salt crystals and, thus, hypersaline conditions. Sulphur stable isotope ratios in pyrite crystals from zone 1 of unit 4 are indicative of high rates of evaporation (R. Morton, pers. comm., 1987). Regional correlation of unit 4 with northern and southern sandstones units suggests that unit 4 was deposited in an embayment, and could have formed one or more restricted basins (Palonen, 1976).

Although the sandstone beds contain dense assemblages of *Skolithos*, the thin sandstones and mudstones contain a very low density and low diversity assemblage of ichnofossils. The only ichnotaxon present in any abundance is *Planolites*. Only rare occurrences of trilobite trace fossils and complex deposit-feeding traces were found. The lower diversity ichnofossil assemblages are consistent with an environment experiencing abnormal or fluctuating salinity (Ekdale *et al.*, 1984). These conditions are generally inimical to marine animals, which have a limited ability to maintain their internal osmotic pressure independently of their environment (Ekdale *et al.*, 1984). The presence of dense, monotaxonomic assemblages of ichnofossils is common in these environments as those animals that can tolerate these conditions are free to proliferate without competition from other species (Ekdale *et al.*, 1984).

The transition from zone 1 to zone 3 is the presumed to be result of a marine transgression (Palonen, 1976). The fine grained, flat to low angle laminated sandstones of zone 2 are probably storm washover fans, deposited into the lagoon from the barrier bar. Zone 3 corresponds to the lower part of Palonen's (1976) unit 5, and is attributed to a shallow subtidal environment, similar to unit 2. However, the presence of well developed dune bed-forms, prominent cross-bedding, and abundant tool and scour marks suggest a much higher energy regime. This is reflected in the higher frequency of *Teichichnus* and *Phycodes*, resulting from the exploitation of buried organic rich horizons; the higher frequency of deep *Cruziana* and *Rusophycus*, such as *Cruziana pormensis*, *C. clavata*, and *Rusophycus* ichnosp. 3; and the rarity of surface scraping forms such as *Cruziana goldfussi*. The abundance of surface trace fossils such as *Rusophycus eutendorfensis* and *Diplichnites* on the base of thin quartzite lentils suggests a high rate of sediment accumulation as these traces would have to have been buried quickly to escape reworking.

Unit Five Description

Unit 5 consists of lenticular to subtabular beds of fine grained, tan coloured quartzite with occasional interbeds of well indurated mudstone and thin quartzite beds (figure 15, 16, 21). THe thick quartzite beds comprise two cross-bedding styles: a basal planar cross-set with upper trough cross-bedding, and amalgamated trough cross-bedding (plate 12b). Herringbone cross-stratification is common throughout the unit (see plate 2b). Except for beds within approximately 5–20 m of the boundaries, this unit is barren.

Mudstones near the the lower boundary contain *Palaeophycus striatus*, *P. tubularis*, ?*Palaeophycus*, *Phycodes circinatum*, *P. palmatum* forms A and B, and *Teichichnus rectus* with rare *Planolites montanus* (figure 21). Rare, isolated *Skolithos linearis* form B shafts were found within thin quartzite beds. The frequency and diversity of biogenic structures decreases gradually up section (figure 21). An amalgamated trough cross-bedded quartzite bed with unlined, 5 mm wide *Skolithos* ichnosp. 1 (plate 12b) and a thin mudstone with dense, intertwining *Planolites montanus* (plate 9d) were found near the top of this unit. The shaft tops occur at several reactivation surfaces within the bed and some pass up into overlying shafts.

A seemingly anomalous interval was found mid-way through the zone, consisting of several 5–20 cm thick beds of moderately sorted, clast supported conglomerate. The pebbles are quartzose, white, well rounded, and 2–5 mm in diameter (plate 5c).

Unit Five Interpretation

Palonen (1976) interpreted unit 5 (upper unit 5 in his scheme) to have been deposited in an upper, sand dominated tidal flat environment with migrating tidal channels, essentially the same as unit 1, zone 3.

Unit Six Description

Unit 6 consists of alternating 2–25 m thick intervals of thick quartzites with thin sequences of wavy bedded shales and thin quartzite beds, and 2–7 m thick intervals of interbedded fissile shale, wavy bedded silty shales, siltstones, and quartzite laminae with clusters of thicker quartzite beds (figure 14, 15, 22).

The thick quartzite intervals are characterised by 10–150 cm thick, strongly lenticular to subtabular beds. There are four styles of cross-bedding: single planar cross-sets (plate, 5b); lower planar cross-sets with upper trough cross-bedding; amalgamated trough cross-bedding (plate 5e); and occasional low angle cross-stratification (plate 2d). The quartzite is generally well indurated and fine grained, however, thin zones of poorly indurated to poorly consolidated, coarse-grained, poorly sorted sandstone occur within some cross-bed sets. Lower bedding surfaces are sharp and usually finely irregular, while upper surfaces are sharp and irregularly undulatory. Ellipsoidal load casts, from several centimetres to over a metre in width, are common above thin shale horizons and thick, shaly interbeds (plate 5a). Some thin quartzite beds are indistinctly mottled, suggesting bioturbation. The thick, cross-bedded quartzites show no evidence of biogenic activity.

The thin layers of linsen and wavy bedded shale within the thick quartzite bed zones are similar to the shaly intervals except in thickness. Ichnofossils are less frequent and less diverse than in the thick shaly intervals, however this may be an artifact of the difficulty of extracting large pieces of shale and thin quartzite from a thin horizon with restricted access. The only common trace fossils are *Teichichnus* and ?*Palaeophycus* with minor occurrences of ?*Arenicolites*, *Chondrites* form D, and *Monomorphichnus* ichnosp.

The shaly intervals change up section from well bioturbated, silt dominated deposits, with abundant evidence for shallow water and emergence, to sparsely bioturbated thin quartzite and silty shale dominated deposits with much less evidence for shallow water.

The lowest interval is dominated by thin siltstone beds with less frequent thin quartzites and interbedded wavy bedded shale, siltstone, and quartzite stringers. The lower bedding surfaces of the siltstones and quartzites are sharp. There are abundant 1–10 cm, irregularly shaped load casts, casts of probable surface run off marks (plate 4a), and tool marks, including bounce and hair-like groove marks (plate 5d). Upper surfaces are smooth, flat to broadly undulatory, and commonly show symmetrical ripple forms and millimetre scale interference ripples. The proportion of siltstone decreases up section as does the frequency of the scour marks, small scale interference ripples, and surface run off structures. The upper intervals are composed of wavy bedded, silty to sandy shales with abundant white quartzite stringers and 5–30 mm thick quartzite and siltstone beds. Lenticularly bedded, 5–30 cm thick, trough cross-bedded quartzites occur as isolated single beds and in clusters of closely spaced groups of 2–5 beds. Lower bedding surfaces are sharp and flat, while upper bedding surfaces are smooth and broadly undulatory. Ripple bed forms are common on the upper surfaces of thin quartzites.

The lower two shaly intervals are well bioturbated, however, most ichnofossils are identifiable as discrete forms; severely bioturbated surfaces with amorphous forms and disruptive overburrowing are very rare. The ichnofossils in these two subunits are anomalously small, averaging 5 mm or less in width. This applies to the burrows and complex deposit-feeding traces, such as *Phycodes*, as well as the surface traces such as *Cruziana* and *Rusophycus*. The most abundant forms are *Chondrites* form B, *Cruziana stromnessa*, *Rusophycus eutendorfensis*, *Phycodes palmatum* form A and *Teichichnus rectus* form C, *Monomorphichnus* forms A and B, and *Planolites montanus*. These ichnofossils form dense assemblages on the base of thin quartzites and siltstones. Less common forms are ?*Arenicolites*, *Bergaueria hemispherica*, *B.* ichnosp., *Chondrites* form A, *Didymaulichnus lyelli*, *Diplichnites* forms B and C, *Palaeophycus striatus*, *P. tubularis*, ?*Palaeophycus*, *Phycodes circinatum*, *P.* ?*flabellum*, *Planolites annularis*, *P. beverleyensis*, *Protopaleodictyon*, *Protichnites*, and *Teichichnus rectus* forms A and B. ?*Zoophycos* is seen as vague spreiten-like structures within siltstone beds. *Gordia marina* and *Chondrites* form A often form dense, monotaxonomic assemblages on lower bedding surfaces of thicker quartzite beds. The significance of the presence of *Protopaleodictyon* is discussed in Chapter 2 (see Ichnogenus *Protopaleodictyon*).

The upper shaly intervals are sparsely bioturbated throughout the shales, thin siltstones and quartzites, and on the lower surfaces of some of the thicker quartzites. Ichnofossils occur as discrete, isolated forms, while extensively bioturbated surfaces are extremely rare. The dominant structure is ?*Palaeophycus* which passes through shales, siltstones, and thin quartzites. *Phycodes palmatum* form A and B, *Teichichnus rectus* forms A, B, and C, are common in clusters of thin quartzite beds. *Chondrites* form B occurs as dense burrows along the lining of *Teichichnus* and *Phycodes* in this interval. *Chondrites* forms A, B and D, *Arenicolites*, and ?*Zoophycos* occur within the thin siltstones and sandy shales. *Skolithos linearis* forms A and B occur sporadically within the shaly intervals of unit 6, but never within the thick, cross-bedded quartzites.

The upper shaly intervals are notable in the rarity of certain ichnotaxa that are common in the lower two recessive units. *Planolites* and *Bergaueria* are absent entirely above subunit 6d. Trilobite traces, except for *Monomorphichnus* ichnosp. and small *Cruziana* and *Rusophycus* in subunits 6a and 6c, are very rare and patchily distributed, however the range of ichnospecies represented by these occurrences is large, including: *Cruziana arizonensis*, *C. plicata*, *C.* ichnosp. 4, *C. clavata*, *Rusophycus* ichnosp. 3, *R. rugosa*, *R. cerecedensis*, and *R. navicella*, all of which were found in float, and *Cruziana* ichnosp. 2, *Rusophycus navicella*, *R.* ichnosp. 1, and *R. bilobatum* which were found in section. All these forms occur on the lower surfaces of 1–5 cm thick quartzite beds.

Unit Six Interpretation

Unit 6 records the last major transgression during Gog Group deposition. Although Palonen (1976) envisioned an environment of deposition very similar to that of unit 2, unit 6 at Redoubt Mountain has ichnological and sedimentological evidence for a markedly different environmental setting. Two environmental zones are distinguished.

The lower zone, comprising the lower two shaly intervals (subunits 6a to 6c), is dominated by thinly bedded siltstones fine sandstones and gritty shales. The high silt component of these deposits, together with the abundance of shallow water indicators, such as desiccation cracks and run off marks, suggests an intertidal environment with a nearby source of fine grained terrigenous clastics (i.e. a river or estuary). The preservation of surface traces on thinly bedded siltstones and quartzites suggests some combination of high rates of sediment accumulation and low rates of biological and physical reworking of the substrate. The ichnofossil assemblages are diverse but typically of low density and are characterised by extremely small specimens. Except for *Chondrites*, there is little evidence of deep deposit-feeding. This suggests some form of physiological stress (Ekdale *et al.*, 1984), most likely related to low salinity given the interpreted geographic context.

The upper zone is composed of alternating resistant and recessive intervals. The resistant intervals are composed of very thick beds with a mixture of thick planar cross-sets and amalgamated-trough cross-bedding. These are presumed to be the result of large channels with large migrating sand waves, reworked on top by smaller megaripples (Palonen, 1976).

Upper zone shaly intervals are similar to those of the lower zone except that there are no indications of emergence or shallow water. Thus, this zone may represent a further transgression from the lower zone. It was probably deposited in a shallow subtidal or low intertidal environment, cross-cut by the large channels. Although the overall diversity of ichnotaxa in the upper zone shaly intervals is similar to the lower zone, most forms are extremely rare. The only abundant form is ?*Palaeophycus* with less frequent occurrences of *Phycodes* and *Teichichnus*. Most of the deposits are largely barren; with ichnofossils occurring as discrete, isolated isolated structures. The presence of ?*Palaeophycus* and occasional *Zoophycos*, along with the rarity of surface arthropod trace fossils and the absence of *Planolites* and *Bergaueria*, suggests that the substrate existed in a semi-cohesive state; possibly representing firm ground conditions *sensu* Ekdale *et al.* (1984). Ichnologically, this is reflected by the low density and diversity of ichnofossils although they may also be a result of brackish water conditions, as postulated for the lower zone.

Summary

The Gog Group at Lake Louise was deposited in an intertidal flat to shallow subtidal environment (Palonen, 1976). The alternating recessive and resistant units in the Lake Louise area represent changes in the position of the paleoshoreline (Palonen, 1976; figure 16). Regional correlation of the shaly units with quartzite dominated units to the north, south, and east suggests that the Lake Louise area comprised a large embayment during the deposition of the Gog Group (Palonen, 1976). Unit 1 deposition began with the progradation of coarse siliciclastic from the newly formed uplands to the east. It grades up section from a swash zone environment to an extensive sand dominated tidal flat/channel complex. Unit 1 deepens upward from upper intertidal flats into the shallow subtidal and lower intertidal environments of unit 2. Unit 2 comprises a series of coarsening upward sequences, each attributed to the abandonment and infilling of tidal channels. Ichnologically, unit 2 plays host to a mixed assemblage, including: surface trackways, subsurface deposit-feeding burrows, and the shafts of infaunal filter-feeders. Such an assemblage is characteristic of soft, marginally cohesive muds in an environment subjected to fluctuations between quiet water and hydrodynamically energetic conditions. Gradual shallowing began near the top of unit 2 and continued through intertidal and, possibly, backshore environments at the top of unit 3. Unit 4 comprises deposits inferred to originate in a restricted lagoon, which in turn, grade up through an interval of back barrier washover deposits into shallow subtidal deposits similar to unit 2, following a second marine transgression. However, the presence of deep surface trace fossils and abundant scour marks indicate a higher energy environment. Unit 5 resulted from a third progradational event and comprises tidal flat/tidal channel deposits, similar to the bulk of unit 1. Unit 6 records the third major marine transgression. Lower unit 6 comprises a silt dominated intertidal environment near an estuary or delta, possibly with reduced salinities. These deposits deepen up section into a shallow subtidal, stiff to firm ground environment, cross-cut by large channels.

Bioturbation in the Gog Group, although it is pervasive and extensive, did not form intensely mottled or amorphous bioturbation fabrics. This is true even where several generations of burrowing can be discerned. Two factors appear to be involved: (1) the high rates of sedimentation and subsidence responsible for the accumulation of Gog Group sediments (Young, 1979); and (2) rates of bioturbation which were probably lower than in equivalent modern settings and did not extend as deeply into the sediment. The latter factor can be attributed to the fact that extensive infaunal deposit-feeding behaviours evolved near the base of the Cambrian System (Fedonkin, 1978, 1980) and may not have been well developed at this point in geologic time.

Trilobite Trace Makers

There were at least 3 major groups of trilobites in the Lake Louise area during deposition of the Gog Group. These groups are defined solely by morphologic features recorded in their biogenic structures. No trilobite body fossils were found in the study area. The members of these groups share common anatomical attributes, as represented by morphological features in the trace fossils. However, they do not necessarily represent monophyletic taxa. Group 1 is characterised by wide, strongly developed appendages, similar to exite branches, that were used for digging and furrowing, as represented by *Cruziana furcifera*, *C. goldfussi*, *C. rugosa*, and *Rusophycus rugosa*. Group 2 is characterised by relatively wide, multiclawed telopodite branches that produced medially tapering, fan shaped scratch marks with 4–6 elements, as characterised by *Cruziana* ichnosp. 1, *Rusophycus avalonensis*, *R. jenningsi*, *R. navicella*, and *R.* ichnosp. 3. A consistent difference in size and bunching of scratch marks between *C.* ichnosp. 1, *R.* ichnosp. 3 and the other members of this group suggests that they were made by a distinct subgroup. Group 3 is characterised by pointed telopodites with 1–3 terminal claws and exite branches that could be scraped against the sediment, as characterised by *Cruziana semiplicata*, *C. arizonensis*, *C.* ichnosp. 4, *C. pormensis*, *C. cerecedensis*, *Rusophycus bilobatum*, *R. parallelum*, *C.* ichnosp. 2, *C. plicata*, and *C. clavata*. The wide variety of plan view shapes in this group suggests that it is made up of a number of different trilobite genera. The scratch mark pattern in this group has no unique features which could be used to identify a particular group of trace makers. A consistent difference in size, however, suggests that the last thee members in the above list were produced by a distinct subgroup.

These trilobites, along with the other fauna of the recessive units, would have been displaced during each regression associated with the resistant units. This fauna would then have had to recolonise the area at the start of deposition of each transgressive unit. However, not all types reappeared in each successive transgressive unit (figure 23). Group 3 trace fossils appear in all three recessive units as would be expected from the non-unique nature of these trace fossils. Group 2 also occurs in all three recessive units, however, they are most abundant in unit 2. Group 1 trace fossils are only common in unit 2. The stiff ground environment of unit 6 and the high energy conditions of unit 4 in the Lake Louise area, may not have been suitable for the shallow, surface deposit-feeding activities ascribed to this group. These trilobites were still present in the region at large, however, as shown by the isolated occurrence of *Rusophycus rugosa* in unit 6.

Supplementary Collecting Sites

The Lake O'Hara and Moraine Lake sites were used primarily to obtain a better estimate of the ichnofossil diversity in the study area.

The lithology and sedimentary features of the float blocks at Moraine Lake are similar to those at Redoubt Mountain and are especially suggestive of unit 4. No confident stratigraphic placement of these float blocks could be made however, given the large difference in the thickness of the Gog Group between the two sites and the inaccessibility of the section at Moraine Lake. Comparison of the ichnofossil assemblages is further hampered by a large difference in the sampling bias due to different bedding surface exposure at the two sites. The Moraine Lake site was chosen because the large float blocks offered good exposure of extensive bedding surfaces. However, only those surfaces on very thick quartzite beds were well represented. The Gog Group forms high, shear cliffs at Moraine Lake and blocks of thinner quartzite and shale are destroyed in the fall to the talus slope. The bedding surfaces of thicker quartzites are the very surfaces which were the most difficult to observe at Redoubt Mountain. This difference in exposure bias probably accounts for the greater relative abundance of surface trace fossils observed at Moraine Lake, including *Cruziana, Protichnites, Didymaulichnus, Monomorphichnus, Rusophycus, Bergaueria.* Infaunal deposit-feeding traces, common in the thinly interbedded shales and quartzites at Redoubt Mountain, are largely absent at Moraine Lake. The only trace fossil of this type that is common at Moraine Lake is *Chondrites* form C. This is a result of the fact that *Chondrites* form C is usually found on the base of thick quartzite beds.

The Lake O'Hara deposits are dominated by hard mudstones rather than shales as is the case at the other two sites. The dominant trace fossils in these deposits are unlined and thinly lined, open burrows with fine, well preserved surface ornamentation, such as *Trichophycus*, ?*Palaeophycus*, *Palaeophycus striatus*; unlined shafts such as *Skolithos* *linearis* form A (plate 11e); and deep *Cruziana* and *Rusophycus* with sharply defined, deeply impressed scratch marks such as *Rusophycus cerecedensis* and *R. jenningsi*. Deposit-feeding burrows such as *Planolites* are rare compared to the Redoubt Mountain site. This sedimentological and ichnological evidence suggests that a strongly cohesive substrate, similar to upper unit 6, existed throughout a wide stratigraphic interval of the Gog Group at Lake O'Hara.

ICHNOTAXONOMY AND CHRONOSTRATIGRAPHY

Ichnotaxonomy

Much of the confusion and controversy in ichnotaxonomy stems from the fact that there are no hard and fast criteria for assessing the taxonomic significance of morphological features as the principle of phylogeny, or relationship by descent, serves for biotaxonomy (Fox, 1986). The assessment of the level of significance of any morphological feature to the taxonomy of a trace fossil is still largely a subjective matter (Fürsich, 1974b; Pemberton *et al.*, 1988). Ichnotaxonomy can not be a purely objective morphological system since there are many factors which influence the morphology of a trace fossil, including: trace maker behaviour; sediment consistency; preservation; erosion and deposition; and trace maker anatomy (Fürsich, 1974b; Pemberton and Frey, 1982; Pemberton *et al.*, 1988). It is important, however, that a consistent set of criteria be established, since ichnotaxa are increasingly being used as entities in their own right, for biostratigraphy and environmental interpretation, without reference to comparisons of morphological descriptions. The way in which ichnotaxa are defined affects their significance to these various applications (see Culver *et al.*, 1987), thus, a standard set of criteria for assessing the significance of morphological features to ichnotaxonomy is needed to ensure that studies using ichnotaxa do not produce erroneous or misleading results (see Fox, 1986; Culver *et al.*, 1987).

In most cases, especially at the ichnogeneric level, ichnotaxonomy is set up to reflect the behaviour rather than the identity of the trace maker (Chamberlain, 1971; Fürsich, 1974b; Pemberton and Frey, 1982; Fillion and Pickerill, 1984; Gureyev, 1985; see Chapter 1). There are instances, however, where trace fossils preserve features which are thought to represent taxonomically significant morphological components of the trace makers (Crimes, 1970c; Seilacher, 1970; Gureyev, 1985; Pemberton *et al.*, 1988). These features are often incorporated into the taxonomy of the trace fossils, either because this makes them useful as index fossils (Seilacher, 1970, 1977, 1985; Crimes, 1975a, 1975c; Kolb and Wolf, 1979; Pickerill *et al.*, 1984; Hakes, 1985) or because they are the only distinct morphological features available (see Seilacher, 1970; Pemberton *et al.*, 1988). As well, some trace fossils provide valuable insights into otherwise unpreservable animal groups (Osgood, 1970; Pemberton and Frey, 1982). Thus, there are strong incentives for incorporating trace maker identity into ichnotaxonomy. This is especially prevalent at the ichnospecific level; and especially for trace fossils for which the inferred trace makers are thought to have chronostratigraphic utility. The prime examples of this are the trilobite trace fossils *Cruziana* and *Rusophycus* (Seilacher, 1970; Crimes, 1975c).

However, as explained in Chapter 1, there is no necessary correlation between biotaxa and ichnotaxa. The use of these two different, often divergent sets of criteria for delineating ichnotaxa seriously hinders the effectiveness of ichnotaxonomy (Gureyev, 1985; see also Culver *et al.*, 1987). This problem is exacerbated by the fact that the representation of anatomical features in the morphology of trace fossils is inconsistent and and often misleading (see Ichnogenus *Cruziana*, Ichnotaxonomy). Most authors are of the opinion that ichnosystematics, at the ichnogeneric level at least, should not be influenced by the identity of the trace maker, especially where the resulting system would conflict with patterns of morphology or ethology (Osgood, 1970; Crimes, 1975a, 1975b; Bromley and Asgaard, 1979; Pemberton and Frey, 1982; Fillion and Pickerill, 1984; Gureyev, 1985). Thus, knowledge of the trace maker identity should not be used in ichnotaxonomy.

If trace fossils do provide valuable data concerning trace makers there should be, as proposed in Ekdale *et al.* (1984), a separate biotaxonomic classification of trace fossils. If such a formal system were set up, however, it would still have to be distinct from the biotaxonomy of body fossils. Although trace fossils may preserve features reflecting the anatomy of the trace maker, in practice it is usually impossible to identify the trace maker to the specific or generic level without comparative body fossils in the same deposits (Bergström, 1973; see Ichnogenus *Cruziana*, Ichnotaxonomy). Trace fossil morphology reflects the trace maker's anatomy to a much smaller extent than its behaviour (Fürsich, 1974a). Only a few ichnotaxa can be confidently assigned to low level biological taxa, and only when representatives of those biological taxa are present in the same deposits (Chamberlain, 1971; Bergström, 1973). The most that a biotaxonomic classification of trace fossils could achieve in a majority of cases is a recognition of a certain number of distinct biotaxa responsible for a taxon of trace fossils in a certain deposit. It would differentiate between a number of different trace makers without actually correlating these to recognised biotaxa. The occurrence of the same ichnotaxon in a different stratigraphic or geographic locality can not independently be used to imply the presence of the same taxa of trace maker (Bergström, 1973). This has serious implications for the chronostratigraphic utility of trace fossils (see below).

Thus, ichnotaxonomy should reflect behaviour (Fürsich, 1974b; Pemberton and Frey, 1982; Ekdale *et al.*, 1984), while remaining true to morphological relationships between actual specimens (Pemberton and Frey, 1982), i.e. ichnotaxonomy should produce natural groupings based on behaviourally significant morphology. However, there is still the problem of how to assess the significance of behaviourally related morphological features for classification at different levels within ichnotaxonomy (Fürsich, 1974a; Pemberton *et al.*, 1988).

Behaviour patterns are, at least to some extent, genetically controlled (Fürsich, 1974a; Gould, 1982). There are two aspects of behaviour: the instinctive and learned behaviour programs stored in the central nervous system and the expressed behaviour of an animal resulting from the interaction of a number of these programs in response to certain environmental stimuli (Gould, 1982). Fürsich (1974a; 1974b) proposed that ichnogeneric level classification be based on morphologic features that reflect the basic behavioural programs that produce the traces, termed significant features, such as the basic program to make open furrows producing *Cruziana*. Ichnospecific level classification would be made on the basis of accessory features, features that reflect the specific interactions of the basic behavioural programs with particular environmental conditions and specific purposes. For example, *Cruziana* ichnosp. 4 and *Cruziana plicata* can be distinguished by the deep, transverse scratch marks of *Cruziana* ichnosp. 4, reflecting slow deep furrowing and the oblique shallow scratch marks of *Cruziana plicata* reflecting shallow fast furrowing (see Crimes, 1970c). One might also add to this strategy that accessory features include features reflecting the interaction of the basic behavioural programs with the specific functional morphology of the trace maker, as it relates to the trace. This is important as the specific morphology of the body parts used to perform an action affect the mechanics of the production of the resultant trace. For example, *Cruziana plicata* and *Cruziana rugosa* are differentiated by the fact that the wide, multiclawed appendage branch of the *Cruziana rugosa* trace maker necessitated a short, longitudinal digging stroke while the narrow, pointed appendage of the *Cruziana plicata* trace maker enabled it to make longer, more oblique digging strokes. However, while this strategy has been utilised by some other ichnologists (Pemberton and Frey, 1982; Pemberton *et al.*, 1988), it has yet to be universally applied in ichnotaxonomy.

One of the unique features of ichnotaxa, compared with biotaxa, is that they often intergrade with each other within single specimens (Crimes, 1970c; Bromley and Frey, 1974; Osgood and Drennen, 1975; Bergström, 1976; Pemberton and Frey, 1982; Pickerill *et al.*, 1984; Seilacher, 1985). This poses certain taxonomic problems. The strategy adopted by most authors in these cases is to give the entire structure the name of the dominant element (Bergström, 1976; see also Pemberton and Frey, 1982; Ichnogenus *Cruziana*). It is the opinion of the author, however, that each component should be named separately, given separate taxonomic treatment, and the interrelationship described. This strategy has three advantages: it simplifies the ichnotaxonomy in a study, although it may lengthen it; it is more consistent with the composite nature of many complex behaviours (Gould, 1982); and it more clearly and effectively conveys ethological and ecological relationships between forms (see above) rather than masking them as does Bergström's (1976) strategy. Since trace fossils represent behaviour, and not actual entities as do body fossils, there should be no philosophical problem in assigning different parts of a single structure to different ichnotaxa. Single organisms do not intergrade, thus single body fossils must always be given a single name. However, different behaviours often, if not normally, grade into each other (Gould, 1982) and the taxonomy of the trace fossils should account for this.

Trace Fossils and Chronostratigraphy

Biostratigraphy is one of the primary sources of data for time correlation — chronostratigraphy (Boggs, 1987). Fossils with chronostratigraphic utility, called index fossils, result from animals which evolved quickly and had geographic distributions which were both extensive and independent of environmental conditions (Boggs, 1987). In contrast, facies fossils, which are used in paleoenvironmental reconstructions, result from animals which evolved slowly and had narrow environmental tolerances (Boggs, 1987). Most good index fossils are from small animals that lived in the water column, as their distributions are geographically extensive and generally independent of bottom conditions, except as it relates to preservation (Boggs, 1987). Most benthic fauna are adapted to their particular substrate and thus, their fossils tend to be restricted to certain sedimentary facies, although they can have a wide geographic distribution through larval dispersal (Boggs, 1987).

Trace fossils can also be used for time correlation (Crimes, 1975c; Ekdale *et al.*, 1984; Narbonne *et al.*, 1987). To produce chronostratigraphically useful trace fossils, an animal should: be active on, or in the sediment; be widely distributed; have wide environmental tolerances; and be rapidly evolving (Crimes, 1975c). Many trace fossils have cosmopolitan distributions (Crimes 1975c; Ekdale *et al.*, 1984; Narbonne *et al.*, 1987) and some of these forms also have restricted time ranges on a period or epoch level (Narbonne *et al.*, 1987). However, trace fossils, being the result of the activities of benthic animals, are usually restricted to certain facies (Ekdale *et al.*, 1984). Even if the trace makers lived in a wide variety of environments, their traces may still be facies restricted as an animal may only perform a given behaviour under certain conditions.

Body fossils are efficacious tools for chronostratigraphy because species have short time ranges and evolve only once (Boggs, 1987). Trace fossils reflect animal behaviour and except in a broad sense, the evolution of behaviour is not of fine enough resolution nor well enough understood to be of use in most precise biostratigraphy. Moreover, because of their highly functional aspect, trace fossils exhibit a high degree of convergence in their evolution. Specific behaviours typically evolve repeatedly over geologic time and have long time ranges, up to the entire Phanerozoic (Ekdale *et al.*, 1984; Gureyev, 1985). This is a result of the fact that there are a limited number of behavioural solutions for any given physiological problem; the fact that many different animals can perform the same function; and that trace fossils reflect the morphology of the trace maker to only a small degree

(Osgood, 1970; Crimes, 1975c; Ekdale *et al.*, 1984). Thus, different occurrences of the same ichnospecies of trace fossil can not be assumed to be of the same geologic age (Bergström, 1973).

Dispersal patterns have an important effect on the chronostratigraphic utility of biostratigraphic zones (Boggs, 1987). Migration and local extinction can create widely differing stratigraphic distributions of the same taxon in different geographic regions (Boggs, 1987). This effect is likely to be accentuated in trace fossils since benthic animals often have slower and more constrained dispersal patterns. Another disadvantage of trace fossils is their large size and generally low density in section. This makes them unsuitable as precise chronostratigraphic markers since any lowest or highest occurrence in section is likely to be several centimetres or even tens of centimetres off the true lowest or highest occurrence.

In spite of these problems, trace fossils may be chronostratigraphically useful in some situations. Some stratigraphic intervals are dominated by siliciclastic facies on a global scale; particularly the Precambrian-Lower Cambrian boundary, as well as Cambrian to Ordovician transition to a lesser extent (Crimes, 1975c). These facies are characteristically impoverished in body fossils, making trace fossils the only potential biological candidates for time correlation (Crimes 1975c; Ekdale *et al.*, 1984; Narbonne *et al.*, 1987). Moreover, there is empirical evidence that many trace fossils, at both the ichnogeneric and ichnospecific levels, have broad facies associations (Narbonne *et al.*, 1987). This is probably a result of the fact that many different types of trace maker can produce the same trace fossil. Another advantage of trace fossils as chronostratigraphic markers is that they are not subject to post production transport (Ekdale *et al.*, 1984). Body fossils are often subjected to post-mortem stratigraphic displacement, either leaking down structural defects in the rock or by biogenic reworking into younger or older sediment (Ekdale *et al.*, 1984). One can conclude, then, that although trace fossils are poor index fossils in general, in some situations they have a good potential for time correlation (Crimes, 1975c; Ekdale *et al.*, 1984; Narbonne *et al.*, 1987).

Ichno-chronostratigraphy

There are three ways in which trace fossils can be used in chronostratigraphy: tracing the evolution of behaviour; as morphologically defined entities with no assumptions concerning their genesis; and as substitutes for the trace making animals.

Evolution of Behaviour

Trace fossils can be used to track the evolution of behaviour, which in itself may be of chronostratigraphic significance. Certain trends in behavioural evolution have been identified which could be of use in gross stratigraphy. These include the increasing complexity and decreasing size of pascichnia through the Paleozoic; the shift of pascichnia and agrichnia, especially graphoglyptids, from shallow subtidal and epeiric settings into the deep sea and high energy beach environments during the early Paleozoic; the shift from predominantly shallow burrowing and surface furrowing to deep burrowing at the base of the Cambrian; and the first occurrence of deep and extensive burrowing in fresh water settings during the late Paleozoic (Crimes, 1974, 1975c; Seilacher, 1974, 1977a; Ekdale *et al.*, 1984; Crimes and Anderson, 1985). Trace fossils are suited for correlating major stratigraphic horizons, such as the basal Cambrian boundary, since major changes in the diversity and composition of animal life should result in major changes in behaviour patterns. As an example, the evolution of mineralised skeletons, articulated appendages, and segmented coeloms near the start of the Cambrian Period resulted in the appearance of deeper and more complex trace fossils than are seen in Precambrian deposits (Crimes, 1975c; see Precambrian-Cambrian Boundary).

The use of behavioural evolution for small scale chronostratigraphy is highly problematical however. Behaviour patterns often evolve repeatedly through geologic time resulting in multiple stratigraphic occurrences of the same trace fossil with no necessary genetic relationship between different occurrences (Ekdale *et al.*, 1984; Gureyev, 1985).

Morphological Entities

Trace fossils can be chronostratigraphically useful as empirically determined distributions of purely morphologically distinguished entities, with no implications for behaviour or trace maker identity. Any entity, biological or otherwise, which can be empirically demonstrated to have a stratigraphically restricted range can be used in applied chronostratigraphy. This is analogous to the use of conodonts for chronostratigraphy before their biological significance was fully understood. Some examples of such chronostratigraphically useful trace fossil distributions are the restriction of *Oldhamia* to the Cambrian of the British Isles (Crimes, 1975c) and the restriction of *Phycodes circinatum* to the Lower Ordovician in Europe (Crimes, 1969, 1975c). Trace fossils can also be useful for defining local marker beds as long as the absence multiple occurrences is well documented (Ekdale *et al.*, 1984). A good example are dense *Ophiomorpha* horizons which can be isochronous over large areas (Ekdale *et al.*, 1984). However, the distribution of such entities, because its significance is not known, can not be used with confidence outside the original area and stratigraphic range where it was defined without an independent means of assessment. This need for caution is demonstrated by the occurrence of *Phycodes circinatum* in the Lower Cambrian Gog Group.

Trace Maker Identity

Trace fossils can be used as substitutes for recognised or hypothetical trace makers. As such, they are used as biological entities for chronostratigraphy in the same way as body fossils. This approach is most useful in siliciclastic facies where body fossils have a poor preservation potential and for trace makers that have a poor preservation potential, such as those without mineralised skeletons (Ekdale *et al.*, 1984). Trace fossils can provide evidence for the first occurrence of certain animal groups, especially at higher taxonomic ranks, in the absence of body fossils. A good example of this is the first occurrence of trilobite trace fossils in arenaceous deposits near the base of the Cambrian, which is used to imply the first occurrence of trilobites in these settings (Crimes, 1975c; Ekdale *et al.*, 1984; Narbonne *et al.*, 1987).

Some trace fossils are used to differentiate the identity of the trace makers to generic or specific levels, for precise chronostratigraphy (Seilacher, 1970; Crimes, 1975c). In many cases the actual trace maker is not known and is assumed to be a unique, although undiscovered taxon (Seilacher, 1970). The best chronostratigraphic ichnospecies are proposed to be those of trilobite trace fossils since trilobites were benthically active; trilobite species had short time ranges; and the trace fossils preserve details of the appendage morphology and plan view size and shape (Seilacher, 1970; Crimes, 1975c). Seilacher (1970) goes so far as to claim that ichnotaxonomy of trilobite trace fossils should exclusively reflect the identity of the trace makers to make them better chronostratigraphic tools. Figures 24 and 25 show the distribution of known trilobite ichnotaxa and gives an indication of their apparent chronostratigraphic usefulness.

The identification of trace makers from their traces is extremely problematical however, even at the phylum and class level (Bergström, 1973; Ekdale *et al.*, 1984). The identification of trace makers down to the genus or family level can be extremely misleading (Bergström, 1973), and only a small number of ichnotaxa can be confidently assigned to low level biotaxa (Chamberlain, 1971; Bergström, 1973). In most cases, assignment to lower level biotaxa can only be made in a relative sense, determining a minimum number of biotaxa responsible for a group of ichnospecies. This may be of use for ecological investigations but is of little use in large scale chronostratigraphy. Confident assignment to particular lower level biotaxa can only be made when representative body fossils are available in the same rocks (Bergström, 1973), in which case the trace fossils become superfluous as index fossils.

The anatomical features responsible for trace fossils are highly functional by their very nature. Such anatomical features are generally stable over evolutionary time, even remaining unchanged through speciation events (Boardman *et al.*, 1987). For example, the wings of different species of birds are not substantially different in their construction or appearance. Moreover, functional anatomy often exhibits a high degree of convergence between unrelated taxa (Boardman *et al.*, 1987). Thus, as stated by Bergström (1973) two geographically or stratigraphically isolated occurrences of the same ichnotaxon can not be used to imply the presence of the same taxon of trace maker. Differentiation between biological species is best made on the basis of non-functional rather than functional attributes, specific patterns in ammonite septal fluting for example, since these features are free to evolve rapidly (Boardman *et al.*, 1987). These features are usually either poorly or misleadingly represented in trace fossils or, as in the case of trilobite appendages, their significance to the taxonomy of the trace maker is poorly understood (G. Edgecombe, pers. comm., 1987). Thus, trace fossils are unsuited for differentiation between low level biotaxa and thus, unsuited as substitutes for body fossils in precise chronostratigraphy on a global scale or over long time ranges. This contradicts the apparent chronostratigraphic utility of *Cruziana* and *Rusophycus* ichnospecies shown in figures 24 and 25. However, many of these stratigraphic distributions have been established in geographically or stratigraphically restricted studies and have yet to be tested over wide geographic or geochronologic ranges. Figure 27 compares the stratigraphic range of the ichnospecies of *Cruziana* and *Rusophycus* found in this study of the Gog Group with their accepted stratigraphic ranges in the literature. Many of the occurrences in the Gog Group are at odds with the previously reported ranges. This shows that much more extensive investigations into the stratigraphic ranges of ichnotaxa on a global scale are needed before they can be used as global index fossils. Many of the stratigraphic distributions in figures 24 and 25 remain efficacious tools for local chronostratigraphy however, within the areas in which they were originally determined. Thus, the author does not advocate wholesale abandonment of trace fossils for this type of chronostratigraphy. They should, however, be treated as morphologic entities (see above), rather than as substitutes for index body fossils.

Applied Ichno-chronostratigraphy

There are two stratigraphic intervals in which trace fossils have a good potential for chronostratigraphic use: the Precambrian-Cambrian boundary and the transition from the Upper Cambrian to Lower Ordovician (Crimes, 1975c). Both of these intervals are composed mainly of siliciclastic deposits in many areas, impoverished in body fossils but containing diverse assemblages of abundant ichnofossils (Crimes, 1975c).

Upper Cambrian-Lower Ordovician Boundary

Crimes (1968) found that the highest occurrence of *Cruziana semiplicata* was roughly coincident with lowest occurrence of *Cruziana furcifera* in northern Wales. This horizon was roughly coincident with Cambrian-Ordovician boundary. Thus, Crimes (1968) reasoned that this ichnological transition might be useful as a stratigraphic marker for the Cambrian-Ordovician boundary. Since that paper, this ichnostratigraphic strategy has been confirmed and refined from investigations in Iberia, the British Isles, and the Avalon Peninsula in Newfoundland, Canada (Crimes, 1969, 1975a, 1975c; Crimes and Marcos, 1976; Baldwin, 1977a; Pickerill *et al.*, 1984; see figure 26). The primary features of this strategy are the last occurrence of *C. semiplicata* and first occurrence of *C. rugosa*, marking the base of the Arenig; and the overlap of *C. semiplicata*, and *C. furcifera* approximating the range of the Tremadoc. This strategy is now used as primary evidence to date Cambro-Ordovician siliciclastic sections (Baldwin; 1977a).

This ichnological strategy was originally developed as an empirically determined stratigraphic distribution of morphological entities within a given area (Crimes, 1968). As such, it has proven quite workable within Baltica and Armorica (Baldwin, 1977a). Many authors (Seilacher, 1970; Crimes, 1975a, 1975c), however, appear to consider the comb-like appendage structure responsible for Rugosa-group *Cruziana* (see *C. rugosa*, *C. furcifera*, and *C. goldfussi*) to be indicative of a unique taxon of trilobites. Thus, these ichnospecies have often been thought of as global Lower Ordovician index fossils. The occurrence of Rugosa-group *Cruziana* in the Lower Cambrian Gog Group shows that this is not the case (figure 27). The time disjunct occurrences of the Rugosa-group in western North America compared with Baltica and Armorica may be the result of the initial evolution of the Rugosa-group making trilobites in western North America and their subsequent migration into Baltica and Armorica before their extinction in North America. On the other hand, these two occurrences could be of no genetic relationship. The appendage structure responsible for these trace fossils is a highly functional attribute and could easily have evolved in a number of unrelated trilobite taxa over geologic time. A similar situation is seen in the highly functional wing structure of bats and pterosaurs, which has evolved independently in both reptiles and mammals. Whatever the case, the presence of Rugosa-group *Cruziana* in the Lower Cambrian Gog Group indicates that these ichnospecies can not be used as global Lower Ordovician index fossils.

Precambrian-Cambrian Boundary

The Precambrian-Cambrian boundary was originally defined as the first occurrence of trilobites (Alpert, 1977). It was subsequently redefined as the first occurrence of archaeocyathans when diverse, typically Phanerozoic faunas were found below the lowest occurrence of trilobites on the Siberian Platform (Narbonne *et al.*, 1987). However, these skeletal fossils are restricted to carbonate dominated facies and thus, have a low potential for global correlation since most Precambrian-Cambrian successions are dominated by siliciclastic deposits (Narbonne *et al.*, 1987).

The current consensus of the Precambrian-Cambrian Boundary Working Group (I.U.G.S.) is that the boundary should be placed at the first occurrence of diverse assemblages of small shelly fossils (Crimes, 1987; Narbonne *et al.*, 1987; Zhang *et al.*, 1987). There is some disagreement with this concept, with some workers (Zhang *et al.*, 1987) maintaining that the boundary should be placed at an iridium anomaly, coinciding with a major extinction event. This would place the boundary at a higher level than that proposed by the I.U.G.S. working group. The working group, however, maintains that the base of the Cambrian should reflect the first appearance of Phanerozoic faunas. Small shelly fossils are good index fossils but, like other body fossils, have a low preservation potential in siliciclastic deposits (Narbonne *et al.*, 1987). Moreover, the cosmopolitan forms have been shown to have extremely long time ranges (Narbonne *et al.*, 1987). Thus, in practice, small shelly fossils are also poor index fossils for the Precambrian-Cambrian boundary (Narbonne *et al.*, 1987).

Ichnofossils are generally regarded as being useful for the recognition of the Precambrian-Cambrian boundary (Crimes, 1975c; Ekdale *et al.*, 1984; Narbonne *et al.*, 1987; see Evolution of Behaviour above). They have two advantages over small shelly fossils: most have cosmopolitan distributions and they are not subject to post production transport (Narbonne *et al.*, 1987). Although by their nature, trace fossils would be expected to exhibit a high degree of facies specificity, many are found throughout a wide variety of siliciclastic and mixed siliciclastic and carbonate deposits (Narbonne *et al.*, 1987).

Banks (1970), Alpert (1977), and Crimes *et al.* (1977) noted that the presence of trace fossils that can be ascribed to Phanerozoic animals should be sufficient evidence to date a deposit as Cambrian or younger. Thus, Banks (1970) and Alpert (1977) proposed lowering the Precambrian-Cambrian boundary from the first occurrence of trilobites to the first occurrence of trilobite trace fossils. The consistent occurrence of trilobite trace fossils below the first occurrence of trilobites is assumed to reflect poor preservation potential of trilobites in the basal Cambrian siliciclastic deposits, compounded by a poorly mineralised exoskeleton in early trilobites (Crimes, 1975c).

Many authors have proposed that trace fossils may have an intrinsic usefulness for the correlation of this boundary, based on the evolution of behavioural patterns. Banks (1970) and Fedonkin (1979, 1980) noted that trace fossils should reflect the appearance of mineralised skeletons, segmented coeloms, and well developed neuromuscular and appendicular systems at the base of the Cambrian by the appearance of deeper and more complex burrows. Upper Precambrian deposits, as old as 750 Ma or more, contain low diversity assemblages of simple, unorganised surface trails and shallow, horizontal burrows (Banks; 1970; Cowie and Spencer, 1970; Webby, 1970, 1973, 1984; Crimes, 1975c, 1987; Alpert, 1977; Crimes *et al.*, 1977; Fedonkin, 1979, 1980; Crimes and Anderson, 1985; Narbonne *et al.*, 1987). These studies have also noted that the diversity of these assemblages and the complexity of the trace fossils increases up section towards the Precambrian-Cambrian boundary with an abrupt appearance of complex, three dimensional burrowing at a point near the Precambrian-Cambrian boundary. In many cases the increasing diversity and complexity of Precambrian trace fossils and the sudden appearance of typically Cambrian forms can not be attributed to changes in lithology or inferred paleoenvironment (Crimes *et al.*, 1977; Crimes and Anderson, 1985; Crimes, 1987; Narbonne *et al.*, 1987). Thus, these trends should be useful for global correlation of the Precambrian-Cambrian transition (Crimes, 1987; Narbonne *et al.*, 1987). The first models placed the Precambrian-Cambrian boundary at the first occurrence of complex, three dimensional trace fossils as this best reflected the onset of behavioural patterns typical of Phanerozoic animals (Fedonkin, 1980, Crimes, 1987, Narbonne *et al.*, 1987). Only in sections with a significant disconformity occupying the base of the Cambrian period do trilobite trace fossils occur at the base of the Cambrian System (Narbonne *et al.*, 1987). This provisional strategy was used by several authors throughout the early 1980's (Fritz, 1980b; Crimes and Anderson, 1985; Fritz and Crimes, 1985; Nowlan *et al.*, 1985).

Crimes (1987) produced the first comprehensive global correlation strategy for the Precambrian-Cambrian boundary, based on a study of fifteen Precambrian-Cambrian sections. This strategy involves three trace fossil assemblage zones. Zone 1 consists of low diversity assemblages of simple horizontal and sub-horizontal traces constructed at or near the sediment water interface (Crimes, 1987). Zone 2 consists of diverse assemblages composed of complex two and three dimensional traces formed both at the surface and at depth (Crimes, 1987). Zone 3 is marked by a further increase in ichnological diversity and the first appearance of certain key ichnotaxa, including those made by trilobites (Crimes, 1987). Zone 1 comprises the upper Precambrian, roughly the Vendian series. The Precambrian-Cambrian boundary was placed at the boundary between zones 1 and 2, marking the first appearance of behavioural patterns indicative of Phanerozoic life forms (Crimes, 1987). This transition is generally quite abrupt (Crimes, 1987). Zone 2 corresponds to the lower Tommotian stage and zone 3 to the upper Tommotian and lower Atdabanian stages (Crimes, 1987). The Atdabanian-Tommotian boundary is marked by first occurrence of trilobite body fossils, which roughly corresponds to the first occurrence of the ichnogenus *Cruziana* (Crimes, 1987). This ichnological model of the Precambrian-Cambrian boundary agrees well with the one based on small shelly fossils where mixed carbonate and siliciclastic deposits preserving both fossil types are found

(Crimes, 1987).

This stratigraphic model was refined by Narbonne *et al.* (1987) using a proposed Precambrian-Cambrian boundary stratotype section in Newfoundland, Canada. Narbonne *et al.* (1987) noted that the highest occurrence of *Harlaniella podolica*, a Precambrian trace fossil, is just below the lowest occurrence of *Phycodes pedum*, which is restricted to the lower Cambrian (Narbonne *et al.*, 1987). A similar stratigraphic relationship was noted in several other well known Precambrian-Cambrian sections in China and Siberia (Narbonne *et al.*, 1987). Thus, the horizon marked by the concurrent lowest appearance of *Phycodes pedum* and highest appearance of *Harlaniella podolica* has been proposed as a marker for the Precambrian-Cambrian boundary (Narbonne *et al.*, 1987). A summary of this biostratigraphic model is shown in figure 28.

One of the more interesting phenomena related to the Precambrian-Cambrian transition, from an ethological point of view, is that the first occurrence of trilobite trace fossils is always stratigraphically below the first occurrence of trilobites (Crimes, 1975c). This occurs often enough that is unlikely to be due to preservation alone (Crimes, 1987). One explanation of this is that the trilobite body plan evolved prior to the mineralization of their exoskeleton (Crimes, 1975c). Trilobite trace fossils occurring below the first trilobites are generally shallow and underdeveloped (Crimes, 1975c; Narbonne *et al.*, 1987). This is consistent with their production by trilobites without mineralised skeletons. Such trilobites would be unable to apply digging and propulsion forces efficiently because of a lack of strong muscle anchors and strong connections between the appendages and the ventral body wall (Crimes, 1975c).

Cruziana is generally the last of the trilobite produced trace fossils to appear in section, and usually occurs very close to the first occurrence of trilobite body fossils (Crimes, 1987). This can be explained by the mechanics of formation of incipient *Cruziana*. The combined digging and propulsion forces required by the appendages in the production of *Cruziana* places extremely large shear stresses on the connection between the appendages and the ventral body surface as well as requiring a high degree of coordination of complex limb movements (Whittington, 1980; Whittington and Almond, 1987; see Ichnogenus *Cruziana*, Mechanics of Emplacement). Thus, it is likely that only a trilobite with a well mineralised exoskeleton and a well developed neuromuscular system could produce the *Cruziana* trace.

Chronostratigraphy of the Gog Group

The general practice in the past has been to consider the Gog Group Lower Cambrian and the Miette Group Upper Precambrian, making the unconformity below the Gog Group equivalent to the Precambrian- Cambrian boundary (Young, 1972). While this has proved useful in mapping the southern Rocky Mountains, northern and western equivalents of the Gog and Miette groups are in gradational contact (Young, 1972). Thus, there is no lithological rationale on a regional scale for this arbitrary age assignment (Young, 1972).

Although the Gog and Miette groups are generally impoverished with respect to index fossils, enough can be found to make rough chronostratigraphic determinations (Young, 1972). The Gog and Cariboo groups in the Jasper area contain abundant skeletal and trace index fossils (figure 4). The Hota Formation in the Gog Group and the Dome Creek Formation in the Cariboo Group both contain Lower Cambrian index fossils, including *Bonnia* and *Olenellus* (Young, 1972), similar to the Peyto Member in the Lake Louise area (Palonen, 1976). The Mural Formation can be correlated from the Gog to the Cariboo Group and contains abundant Lower Cambrian skeletal fossils that can be matched between sections, including *Olenellus*, *Judomia*, *Nevadella*, *Fallotaspis*, and archaeocyathids (Young, 1972). The lowest skeletal fossil zone represented in the Mural Formation is the *Fallotaspis* Zone (Young, 1972), indicating a lower Atdabanian age (Harland *et al.*, 1982).

Below the Mural Formation, in both the Gog and Cariboo groups, there is a thin interval (100–150 m) containing diverse, typically Phanerozoic ichnofossils (Young, 1972; figure 4). The nature of the assemblage differs in the two groups as a result of different environments of deposition. It consists of complex horizontal burrows and trails in the deep water gritty shales of the Cariboo Group and vertical burrows and arthropod traces in the shallow water sandstones and shales of the Gog Group (Young, 1972). There are no trace fossils except for rare *Planolites* in the Gog and Cariboo groups below this interval. Young (1972), proposed that although the base of the diverse trace fossil interval is quite abrupt, the wide variety of environments represented below this zone makes it reasonable to assume that the trace makers had not evolved at this point and were not simply absent from this locality. Therefore, the Atdabanian-Tommotian boundary was tentatively placed at the base of the diverse trace fossil interval by Young (1979). The lower Gog and Cariboo groups (below the ichnofossiliferous interval) are within the range of Precambrian metazoa, and possibly within the Tommotian, as shown by the occurrence of *Didymaulichnus miettensis* and small shelly fossils in the Miette Group near Jasper (Young, 1972, 1979; figure 4). Thus, the barren zone and at least the upper part of the Miette Group is within the Tommotian Stage.

However, there is a distinct possibility that the lack of trace fossils below the diverse trace fossil zone is paleoenvironmentally controlled. The Cariboo Group consists of deep water deposits (Young, 1972) and it is generally acknowledged that deep water benthic environments were not extensively colonised until later in the Cambrian (Crimes, 1974; Crimes and Anderson, 1985). The part of the McNaughton Formation below the diverse trace fossil, on the other hand, is dominated by thick quartzites with rare shaly interbeds, and has a poor potential for both the formation and preservation of most trace fossils.

An important factor in the consideration of any time boundary is presence of time diagnostic fossils both above and below the boundary to avoid the possibility of an environmental rather than evolutionary control on absence of a particular fossil in a correlation (Banks, 1970; Bergström, 1970; Narbonne *et al.*, 1987). Young (1972) has no Tommotian index fossils, either skeletal fossils or ichnofossils, within the Gog or Cariboo groups below the diverse trace fossil zone (figure 4). Thus, the first occurrence of *Cruziana*, *Rusophycus*, and other complex traces can only be used as youngest possible base for the Atdabanian Stage in the Jasper region. In the Lake Louise area, trilobite trace fossils occur much farther below the Lake Louise Formation than their first occurrence below the Mural near Jasper. This coincides with the presence of thick intervals of thinly interbedded shales and quartzites lower down in the Gog Group at Lake Louise. Thus, the actual time range of Atdabanian trace fossils probably extends below their lowest occurrence in the McNaughton Formation.

The Mackenzie Mountains contain a Precambrian-Cambrian transition consisting of interbedded sandstones, shales, and carbonates, unlike the thick quartzite dominated deposits of the Gog Group to the south (Fritz, 1980b). These deposits show an ichnological succession similar to the one documented by Crimes (1987) for global correlation of the Precambrian-Cambrian boundary (Fritz, 1980b; Nowlan *et al.*, 1984). This involves a progression from simple surface trails and shallow burrows, typical of Crimes' zone 1, through a zone of more complex traces including *Phycodes pedum* and *Treptichnus*, typical of Crimes' zone 2, into a zone with *Teichichnus*, *Rusophycus*, and *Scolicia*, typical of Crimes' zone 3 (Fritz, 1980b). The Precambrian-Cambrian boundary has been tentatively placed at the base of the second zone (Fritz, 1980b) in agreement with Crimes (1987). The third zone begins at the base of the *Fallotaspis* Zone, corresponding roughly to the base of the Atdabanian Stage (Harland *et al.*, 1982; Crimes, 1987).

Thus, there is a typical Tommotian ichnological assemblage in at least some regions of the western paleocoastline of North America. Its absence in the Gog and Cariboo groups must be a result of its removal by the unconformity below the Gog Group or the result an unsuitable sedimentary setting for its production or preservation. The basal Cambrian unconformity is not extensive enough in all sections to have removed all evidence of a Tommotian Stage, especially in northwestern sections of the Gog and Cariboo groups (Young, 1972, 1979).

The only lithologic unit with time diagnostic skeletal fossils in the Lake Louise area is the Peyto Member which contains the lower Cambrian trilobite *Olenellus* (Palonen, 1976), making it roughly coeval with the Hota Formation in the Jasper area. The units overlying the Gog Group, the Mount Whyte, Cathedral, and Stephen formations, are of Middle Cambrian age (Price *et al.*, 1980a, 1980b). Thus, the Lake Louise Gog Group is Atdabanian in age at its youngest. There are no skeletal fossils for time correlation below the Peyto Member (Palonen, 1976). However, the range of abundant trilobite traces, *Chondrites*, *Teichichnus*, and *Phycodes* extends to the base of unit 2. Therefore, according to Crimes (1987), the Fort Mountain Formation must be of middle Tommotian Age at the oldest, at least to the base of unit 2 (see figure 28). Moreover, the trilobite traces are deep and well developed through out the Gog Group. This suggests that the deposits are as young as, or younger than, the first occurrence of trilobites with mineralised skeletons (Crimes, 1975c; see above). This would place the Gog Group, from the base unit 2 and up, within the Atdabanian Stage (Crimes, 1987).

Unit 1 consists of thickly bedded cross-bedded quartzites with rare shaly interbeds. This facies would not be expected to preserve trace fossils, thus there is no reason to assume that the time range of Atdabanian trace fossils found in in unit 2 does not range into the time of deposition of unit 1. No trace fossils have ever been found in the Miette group in the Lake Louise area, however, no concerted search has ever been made for them (W. Arnott, pers. comm., 1987). The Miette Group may be of Tommotian Age, as in Jasper, or older.

CONCLUSIONS

The Gog Group is a thick, siliciclastic deposit composed of alternating units of cliff-forming, cross-bedded quartzites and recessive, thinly interbedded quartzites and shales. The resistant units comprise the deposits of sand dominated, upper tidal flats with large, laterally migrating tidal channel. These deposits are barren over most of their thickness. However, near their upper and lower boundaries, they contain abundant shafts: *Arenicolites*, *Diplocraterion*, and *Skolithos*, as well as sporadically distributed but locally abundant simple burrows, mostly *Planolites* and *Palaeophycus*. The recessive units contain a diverse assemblage of trace fossils, comprising a wide range of behavioural types, including surface excavations; simple horizontal burrows; complex infaunal deposit-feeding structures; and sporadically distributed shafts. The lower recessive unit comprises a shallow subtidal deposit with soft, marginally cohesive sediments and an ichnofossil assemblage that exhibits the full range of behavioural types. The middle recessive unit grades up from lagoon and washover deposits, with sparse to locally intense bioturbation, into shallow subtidal deposits, similar to unit 2 but with deeper surface trace fossils and more frequent scour marks indicating higher energy conditions. The upper recessive unit consists of silt dominated, shallow subtidal and intertidal deposits with evidence for the development of stiff to firm substrates and reduced salinities.

The Gog Group is of Early Cambrian age, however, the paucity of index body fossils has thwarted most attempts at precise age determinations. The presence of *Olenellus* Zone index fossils in the Peyto Member indicates that the Gog Group is of Atdabanian age at its youngest. The presence of well developed, deep *Cruziana* and *Rusophycus* near the base of the Gog suggests that the entire Gog Group, in the Lake Louise area, is of Atdabanian age since these trace fossils must have been produced by arthropods with well mineralised skeletons. Most of the Tommotian Stage is contained within the sub-Cambrian unconformity. The unconformity at the top of the Peyto Member accounts for all of the Lenian Stage.

Most of the ichnotaxa present in the Gog Group are typical of middle Lower Cambrian siliciclastic deposits. However, there are a number of ichnotaxa in these deposits which are restricted to the Lower and Middle Ordovician in Europe and Newfoundland: *Cruziana furcifera*, *C. goldfussi*, *C. rugosa*, *Rusophycus rugosa*, and *Phycodes circinatum*. These trace fossils have been used as Lower Ordovician index fossils by many ichnologists. Their presence in the Gog Group indicates that, while these trace fossils may be useful as local or basin wide time markers, their stratigraphic distribution on a global scale is not sufficiently understood to use them as global index fossils. The same holds true for most arthropod generated ichnotaxa.

Part of the problem with arthropod produced ichnotaxa stems from the controversy and confusion over what features should be used to define these ichnotaxa. Many trilobite ichnotaxa are defined on the basis of morphological features which are presumed to reflect taxonomically significant anatomical features of the trace makers. These generally consists of patterns in the grouping of scratch marks and presence of such features as marginal ridges. These features reflect patterns of appendicular spines, and cephalic and pleural spines respectively. There are three reasons why this is a poor strategy. In practice, there is no one-to-one relationship between trilobite biotaxa and ichnotaxa. The same ichnospecies of *Cruziana* or *Rusophycus* can occur over stratigraphic and geographic ranges that could not be spanned by a single genus of arthropod. As well, markedly different ichnospecies of these forms often intergrade with each other indicating that one species of trilobite can produce a wide range of ichnospecies of *Cruziana* or *Rusophycus*. Another problem is that the representation of anatomical features in the morphology of the trace fossils is inconsistent, varying with the behaviour of the trace maker and properties of the sediment. Moreover, the significance of these anatomical features to the systematics of trilobites is poorly understood.

FIGURES AND PLATES

Figure 1
Location Map.

North America and Alberta base maps courtesy of Andrew J. Fox. Lake Louise base map redrawn from National Topographic System (Canada) map 82 N/8, Department of Energy, Mines, and Resources Canada.

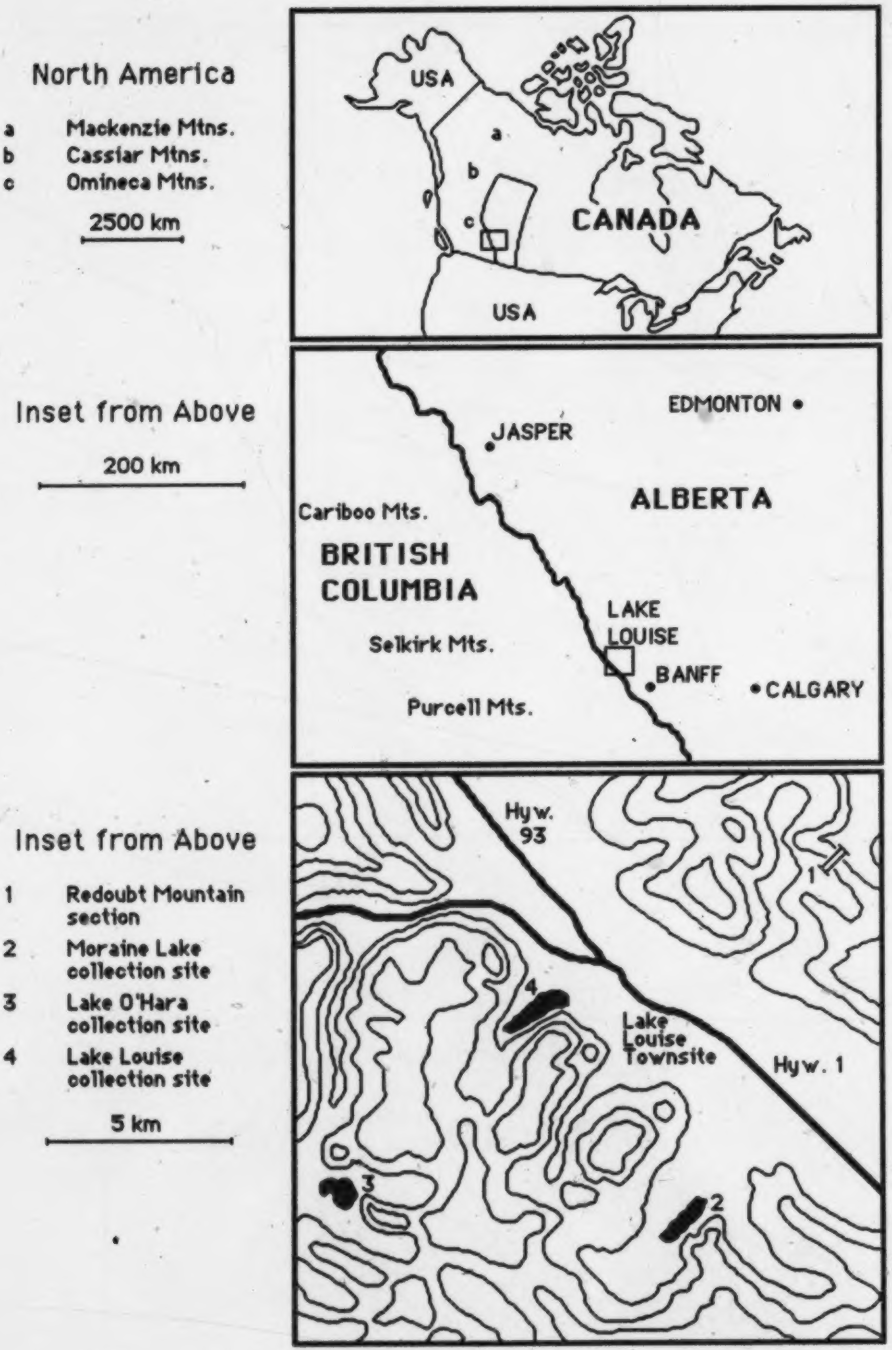

North America
a Mackenzie Mtns.
b Cassiar Mtns.
c Omineca Mtns.
2500 km
USA
a
b
c
CANADA
USA
Inset from Above
200 km
EDMONTON
JASPER
Cariboo Mts.
ALBERTA
BRITISH COLUMBIA
LAKE LOUISE
Selkirk Mts.
BANFF
CALGARY
Purcell Mts.
Inset from Above
1 Redoubt Mountain section
2 Moraine Lake collection site
3 Lake O'Hara collection site
4 Lake Louise collection site
5 km
Hyw. 93
1
4
Lake Louise Townsite
Hyw. 1
3
2

Figure 2

Correlation diagram for Lower Cambrian and upper Precambrian formations of the western Canadian Cordillera. Figure 1 shows the position of each geographic locality.

Redrawn from Wolberg (1986).

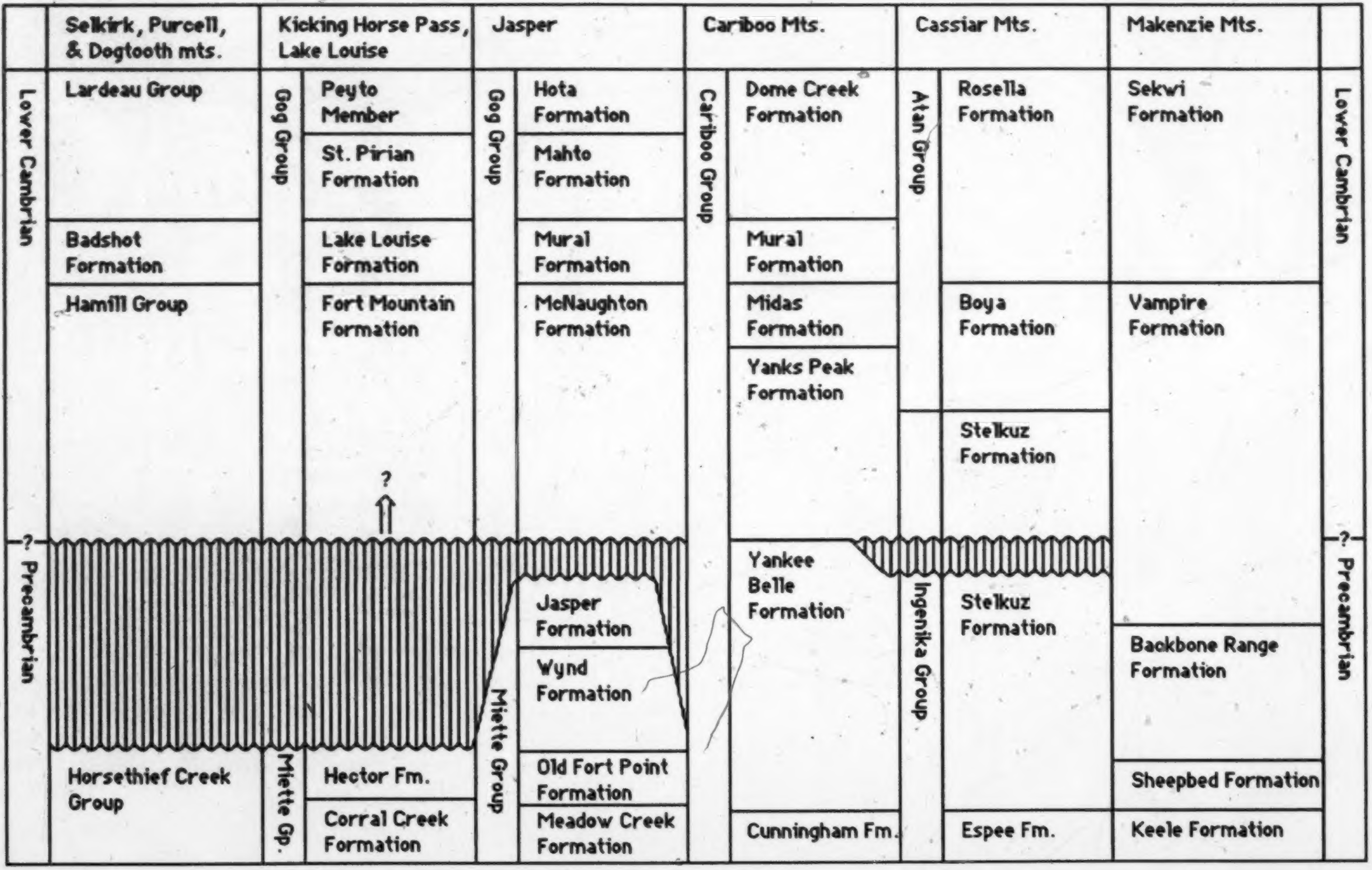

Selkirk, Purcell, & Dogtooth mts.
Kicking Horse Pass, Lake Louise
Jasper
Cariboo Mts.
Cassiar Mts.
Makenzie Mts.
Lower Cambrian
?
Precambrian
Lardeau Group
Badshot Formation
Hamill Group
Horsethief Creek Group
Gog Group
Miette Gp.
Peyto Member
St. Pirian Formation
Lake Louise Formation
Fort Mountain Formation
?
Hector Fm.
Corral Creek Formation
Gog Group
Miette Group
Hota Formation
Mahto Formation
Mural Formation
McNaughton Formation
Jasper Formation
Wynd Formation
Old Fort Point Formation
Meadow Creek Formation
Cariboo Group
Dome Creek Formation
Mural Formation
Midas Formation
Yanks Peak Formation
Yankee Belle Formation
Cunningham Fm.
Atan Group
Ingenika Group
Rosella Formation
Boya Formation
Stelkuz Formation
Stelkuz Formation
Espee Fm.
Sekwi Formation
Vampire Formation
Backbone Range Formation
Sheepbed Formation
Keele Formation
Lower Cambrian
?
Precambrian

Figure 3
Paleogeographic reconstruction of the continents during the Late Cambrian.
Redrawn from Scotese *et al*. (1979).

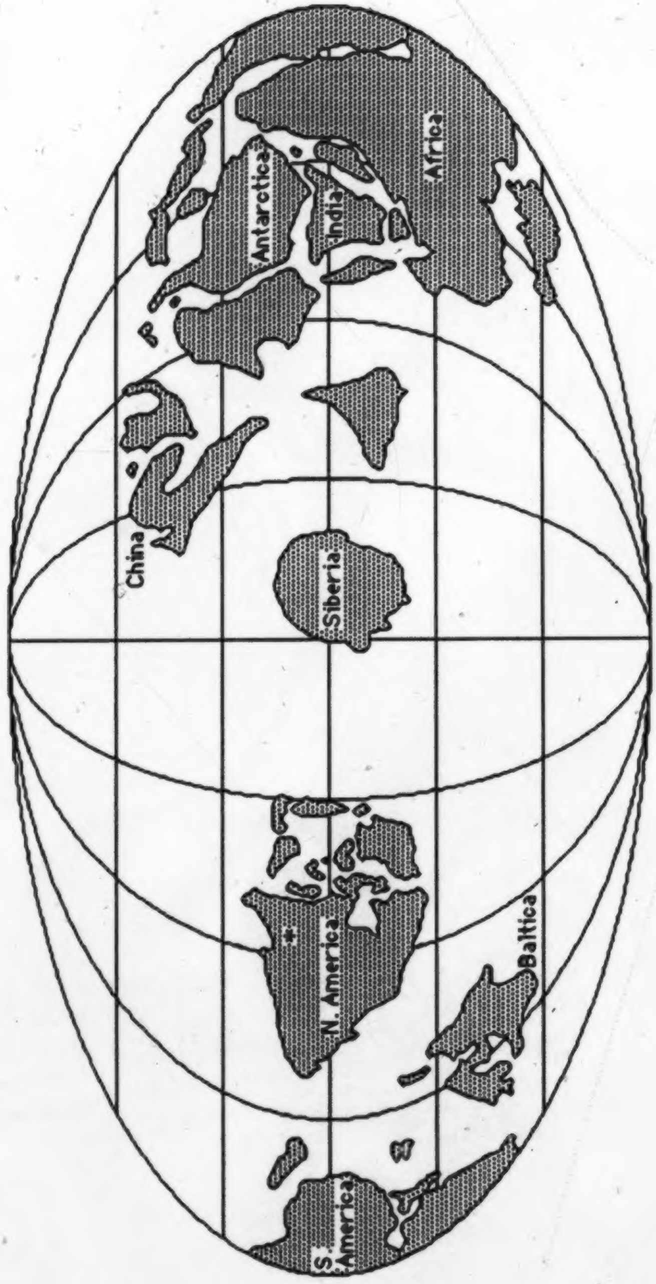
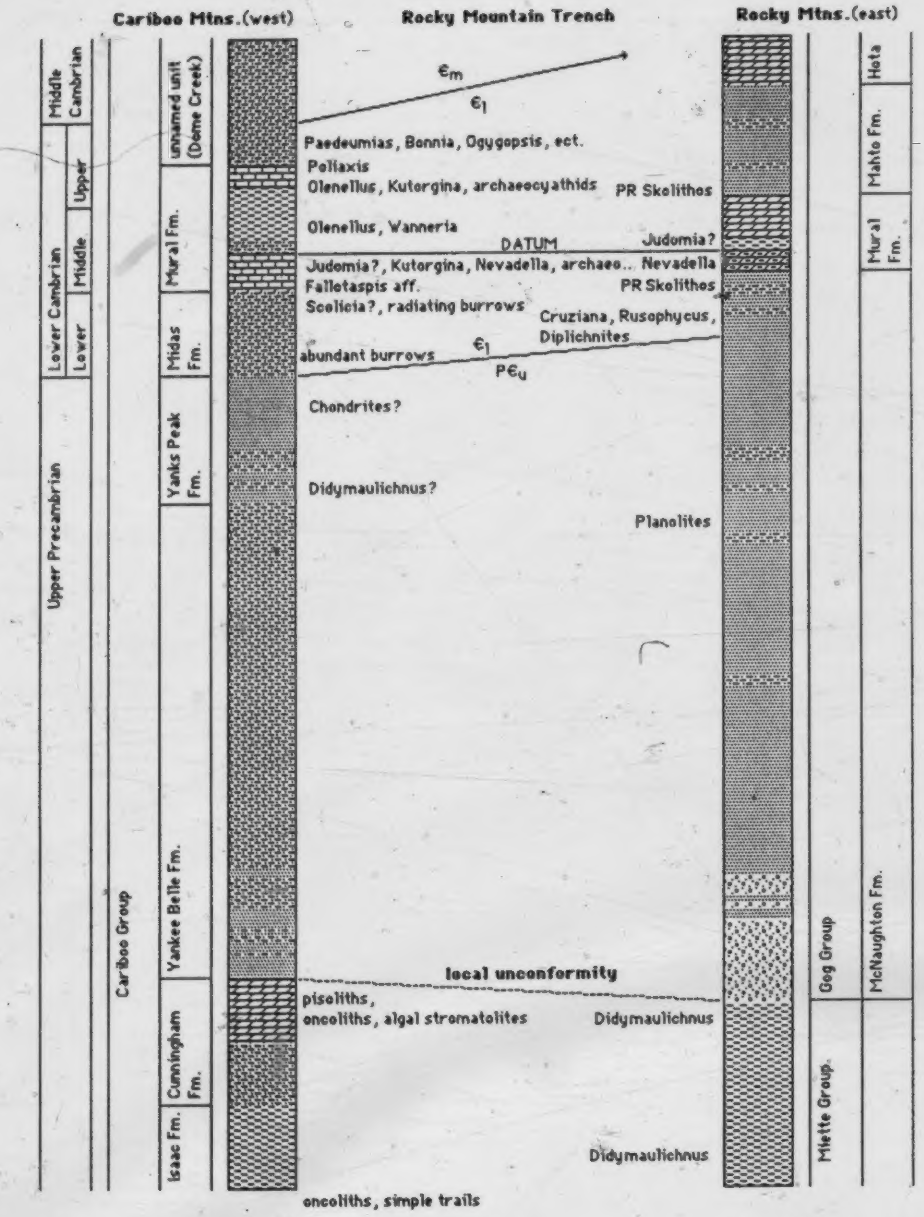

Antarctica
Africa
India
China
Siberia
N. America
Baltica
S. America

Figure 4

Correlation diagram for the Gog, Cariboo, and Miette groups, north of Jasper, Alberta, from Young (1972), showing proposed time boundaries and the positions of important biostratigraphic markers.

Modified from Young (1972, 1979).


Cariboo Mtns.(west)
Rocky Mountain Trench
Rocky Mtns.(east)
Middle Cambrian
Lower Cambrian
Upper
Middle
Lower
Upper Precambrian
Cariboo Group
unnamed unit (Dome Creek)
Mural Fm.
Midas Fm.
Yanks Peak Fm.
Yankee Belle Fm.
Cunningham Fm.
Isaac Fm.
€m
€l
Paedeumias, Bonnia, Ogygopsis, ect.
Pollaxis
Olenellus, Kutorgina, archaeocyathids
PR Skolithos
Olenellus, Wanneria
DATUM
Judomia?
Judomia?, Kutorgina, Nevadella, archaeo..
Nevadella
Fallotaspis aff.
PR Skolithos
Scolicia?, radiating burrows
Cruziana, Rusophycus, Diplichnites
abundant burrows
€l
P€u
Chondrites?
Didymaulichnus?
Planolites
local unconformity
pisoliths,
oncoliths, algal stromatolites
Didymaulichnus
Didymaulichnus
oncoliths, simple trails
Hota
Mahto Fm.
Mural Fm.
McNaughton Fm.
Gog Group
Miette Group

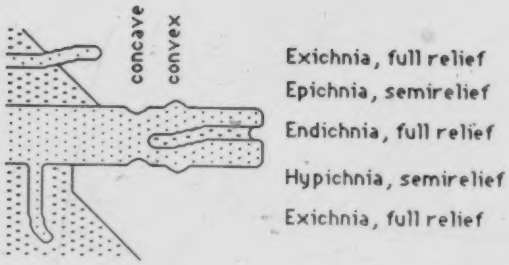

concave
convex
Exichnia, full relief
Epichnia, semirelief
Endichnia, full relief
Hypichnia, semirelief
Exichnia, full relief

Figure 5
The preservational classification of trace fossils.
Modified from Ekdale *et al.* (1984)

Figure 6

Basic morphology of a hypothetical trilobite to show major external features refered to in the text. Only the anterior pygidial appendages have been shown for sake of clarity.

A=antenna; AA=anterior arch; AB=anterior border; CX=coxa; DB=doublure; EX=exite branch; EXF=exite fringe; EY=eye; GB=gnathobase; GL=glabella; GS=genal spine; HY=hypostome; PL=pluron; T=telopoditebranch; TPx=xth podomere of the telopodite branch; VMF=ventro-medial food groove.

Modified from Clarkson (1979), Whittington (1980), Bergström and Brassel (1984), Müller and Walossek (1987).

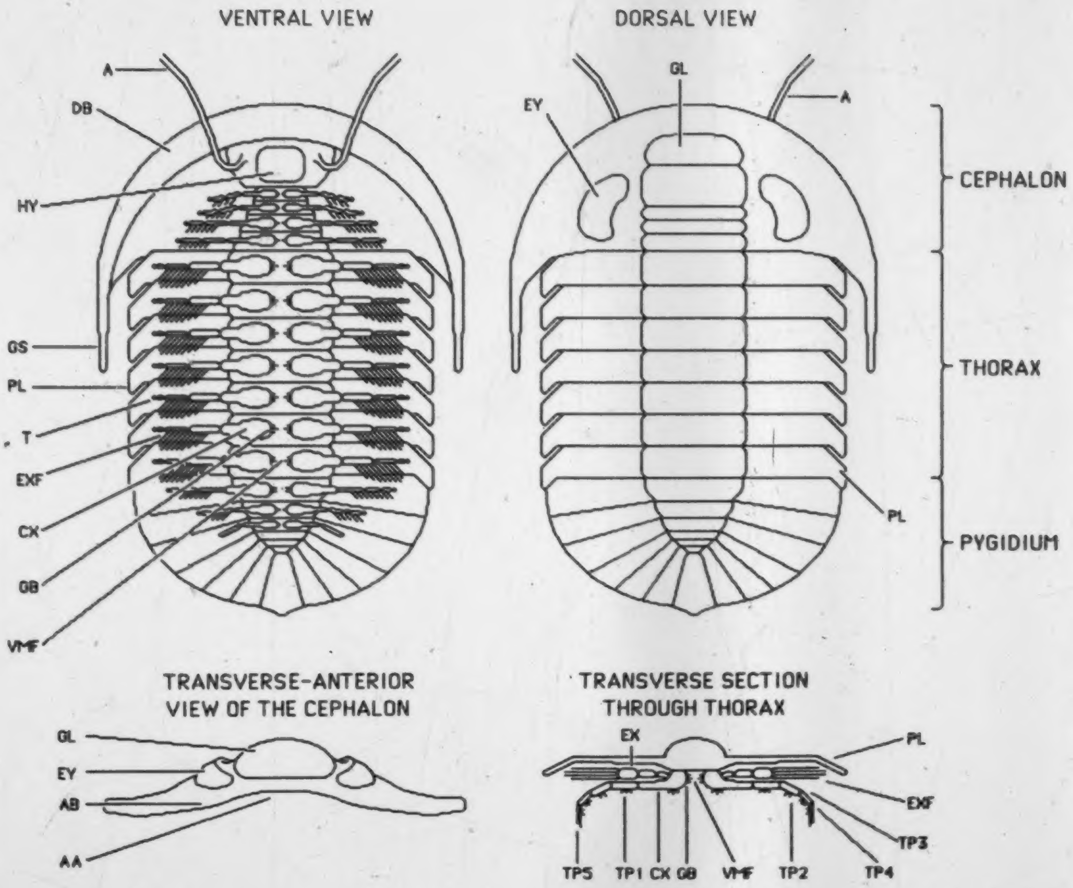

VENTRAL VIEW
A
DB
HY
GS
PL
T
EXF
CX
GB
VMF
DORSAL VIEW
EY
GL
A
PL
CEPHALON
THORAX
PYGIDIUM
TRANSVERSE-ANTERIOR VIEW OF THE CEPHALON
GL
EY
AB
AA
TRANSVERSE SECTION THROUGH THORAX
EX
PL
EXF
TP3
TP4
TP5
TP1
CX
GB
VMF
TP2

Figure 7

Summary of known, reliable trilobite appendage reconstructions in postero-ventral view.

a) *Olenoides serratus* (Whittington, 1980)

a_{ii}) *Olenoides serratus* showing the imbrication of the exite fringes against the top of the next posterior exite fringe.

b) *Cryptolithus* sp. (Bergström, 1972).

c) *Agnostus pisiformis* (Müller and Walossek, 1987).

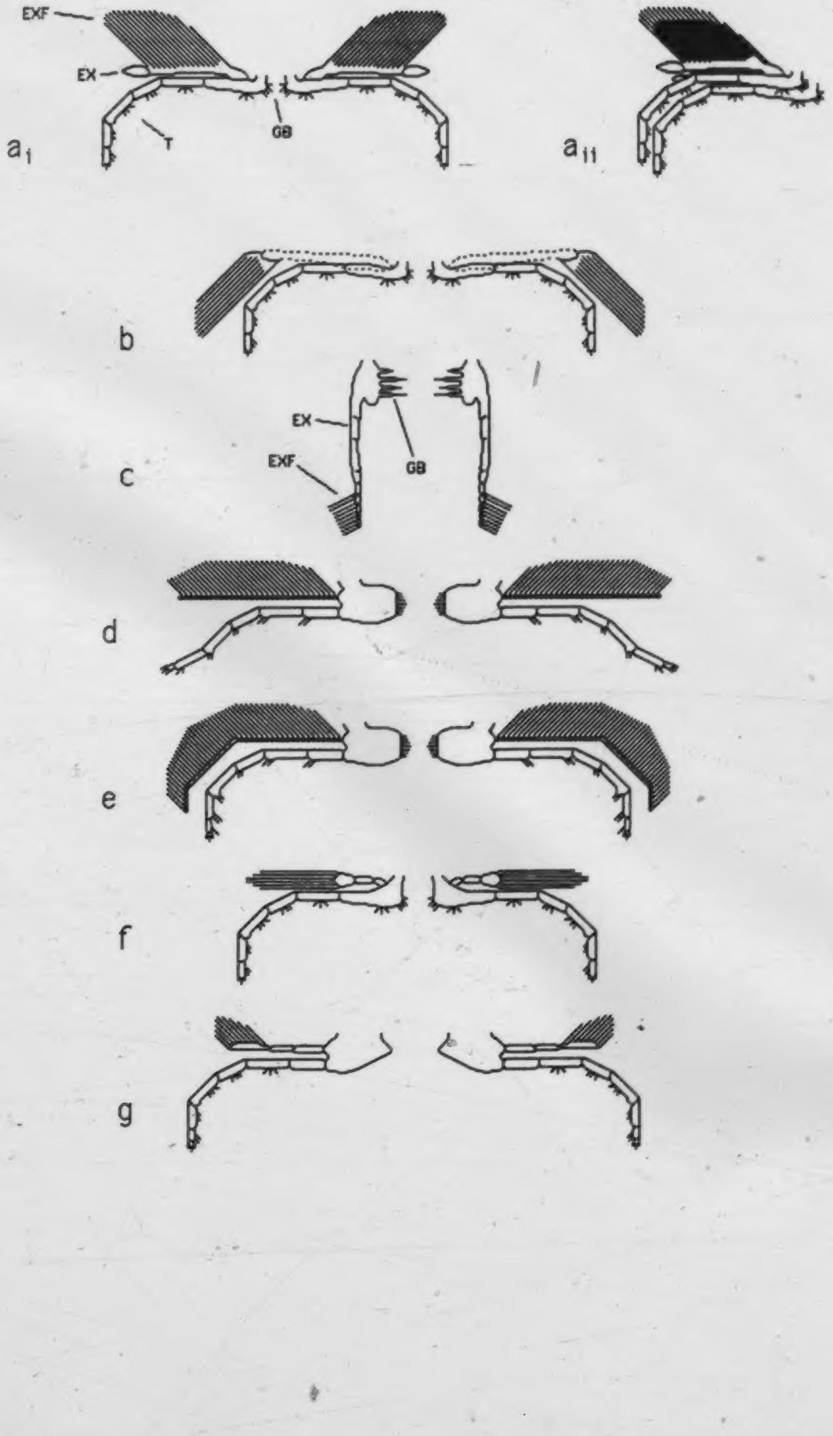
d) *Triarthrus eatoni* (Cisne, 1981).

e) *Triarthrus eatoni* (Whittington and Almond, 1987).

f) *Phacops* sp. (Müller and Walossek, 1987).

g) *Ceraurus pleurexanthemus* (Müller and Walossek, 1987).

EX=exite branch; EXF=exite fringe; GB=gnathobase; T=telopodite branch.


EXF
EX
GB
T
a$_i$
a$_{ii}$
b
EX
GB
EXF
c
d
e
f
g

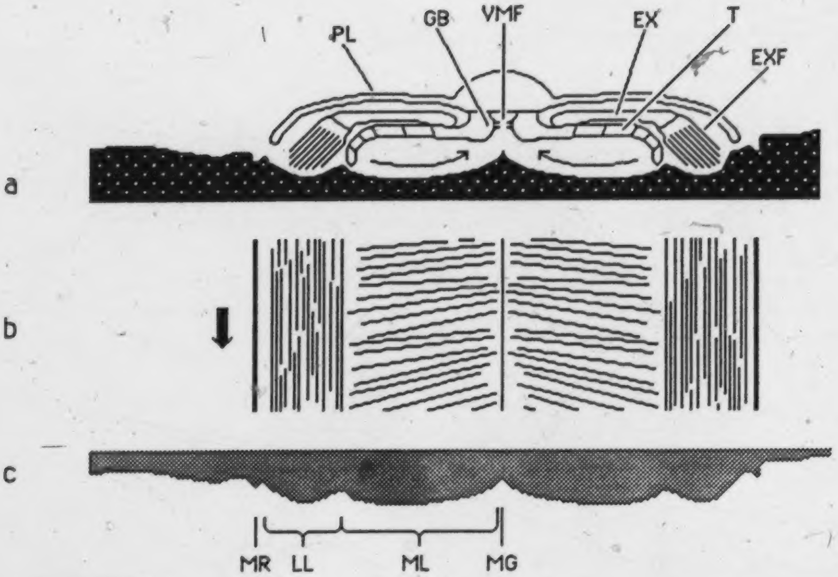


Figure 8

Summary of Crimes' (1975b) model for the production and preservation of *Cruziana*.

a) Action of the appendages in the construction of open furrows in a soft, muddy substrate, seen in transverse-anterior view.

b) surface ornamentation of the resulting trace and subsequently produced trace fossil. The solid arrow shows direction of travel.

c) The trace fossil *Cruziana*, resulting from the casting, lithification, and weathering out of the original furrow, seen in transverse view.

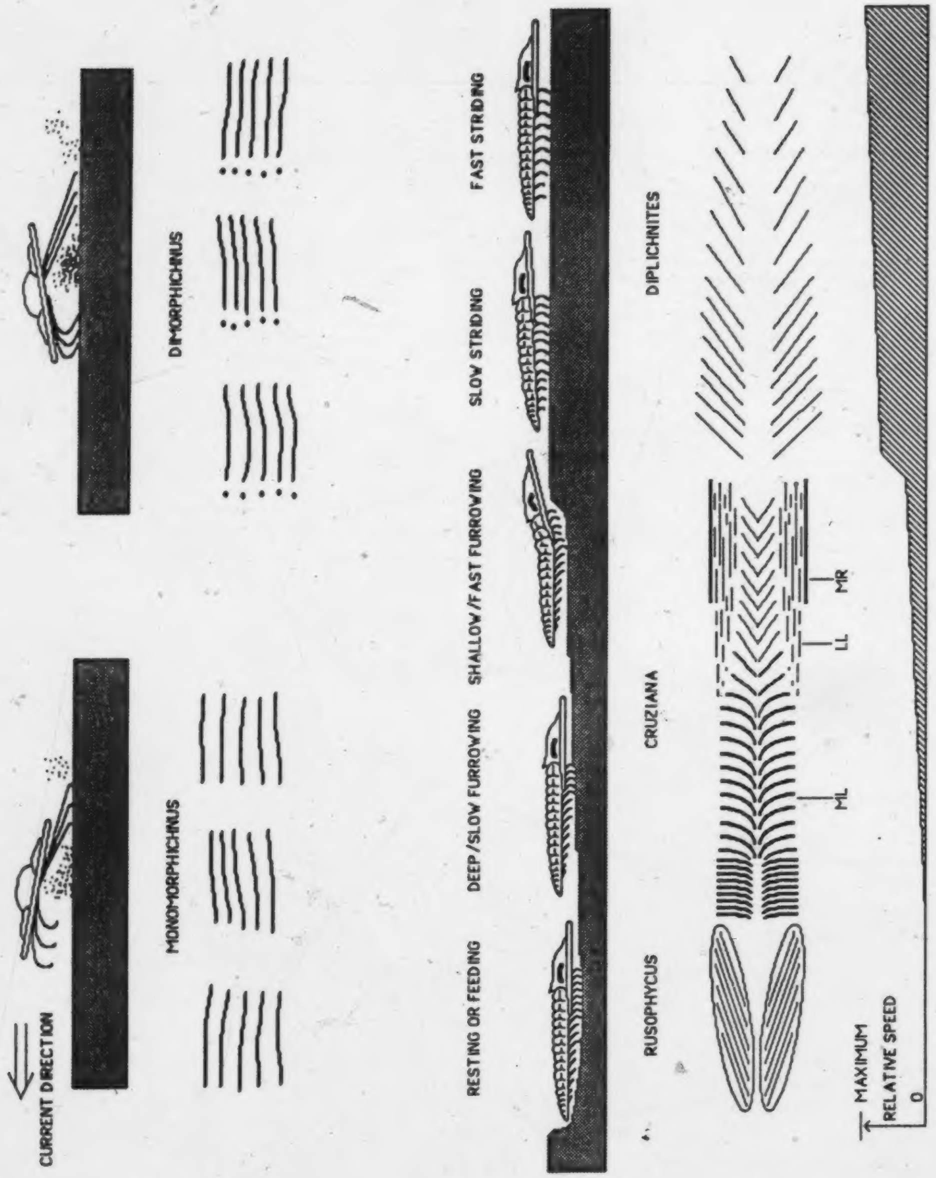
EX=exite branch; EXF=exite fringe; GB=gnathobase; LL=lateral lobe; MG=median groove; ML=medial lobe; MR=marginal ridge; T=telopodite branch; VMF=ventro-medial food groove.

A

Figure 9

A summary of the common trace making activities of trilobites and the resultant ichnofossils.

Redrawn from (Crimes, 1970c).


CURRENT DIRECTION
SWIMMING/GRAZING
SIDEWAYS GRAZING
MONOMORPHICHNUS
DIMORPHICHNUS
RESTING OR FEEDING
DEEP/SLOW FURROWING
SHALLOW/FAST FURROWING
SLOW STRIDING
FAST STRIDING
RUSOPHYCUS
CRUZIANA
DIPLICHNITES
ML
LL
MR
MAXIMUM
RELATIVE SPEED
0

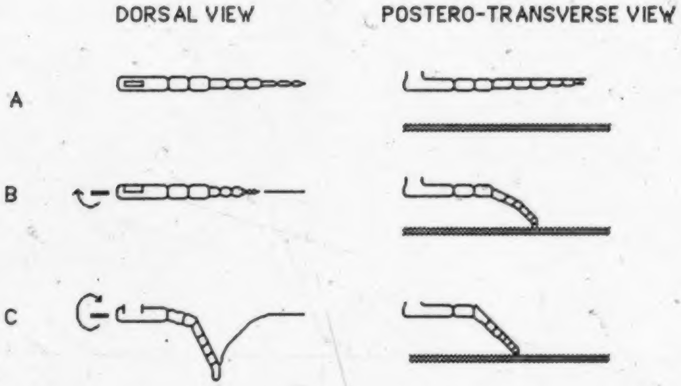


Figure 10

Hypothetical mode of action of the telopodite branch of trilobite appendages in the production of incipient *Cruziana* (from Whittington, 1980).

a) Position of the telopodite before placement on the sediment.

b) Flexation of the telopodite mid way through the inward stroke, providing the digging force.

c) Extension and rotation of the telopodite towards the end of the inward stroke, providing the pushing force.

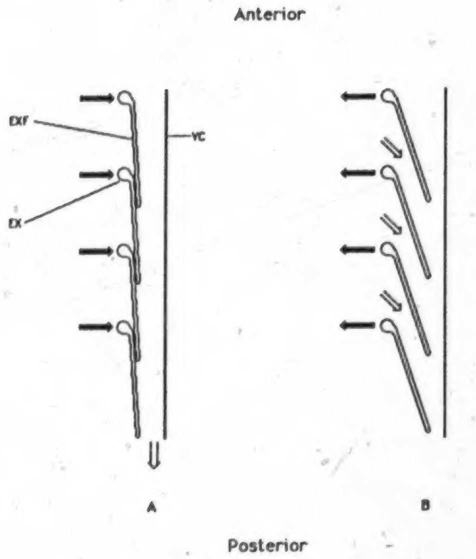


Figure 11

The mechanics of water pumping by the exite fringes during the outward and inward motion of the telopodite branches (see Whittington and Almond, 1987). Diagrams are drawn in parasaggital view.

a) Water is pushed against the ventral body wall and out from under the body (open arrows) as the exites are pushed up and out (solid arrows) during the outward stroke of the telopodites.

b) Water is sucked into the space between the exites and ventral body wall (open arrows) as the exites are pulled down and in (solid arrows) during the inward stroke of the telopodites.

EX=exite branch (in transverse section); EXF=exite fringe; VC=ventral body wall (ventral carapace).

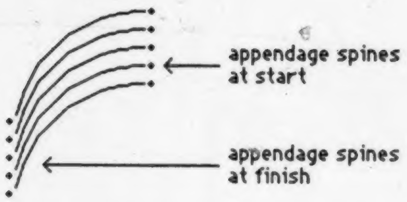

appendage spines at start
appendage spines at finish

Figure 12

The formation of medially bundled, fan-shaped scratchmarks in *Rusophycus avalonensis*. The direction of motion is lateral to medial and front to back.

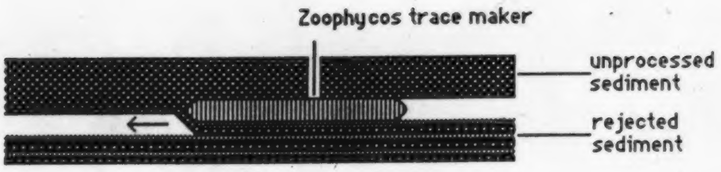

Zoophycos trace maker
unprocessed sediment
rejected sediment

Figure 13
The formation of minor lamellae in *Zoophycos*.
Redrawn from Simpson (1970)

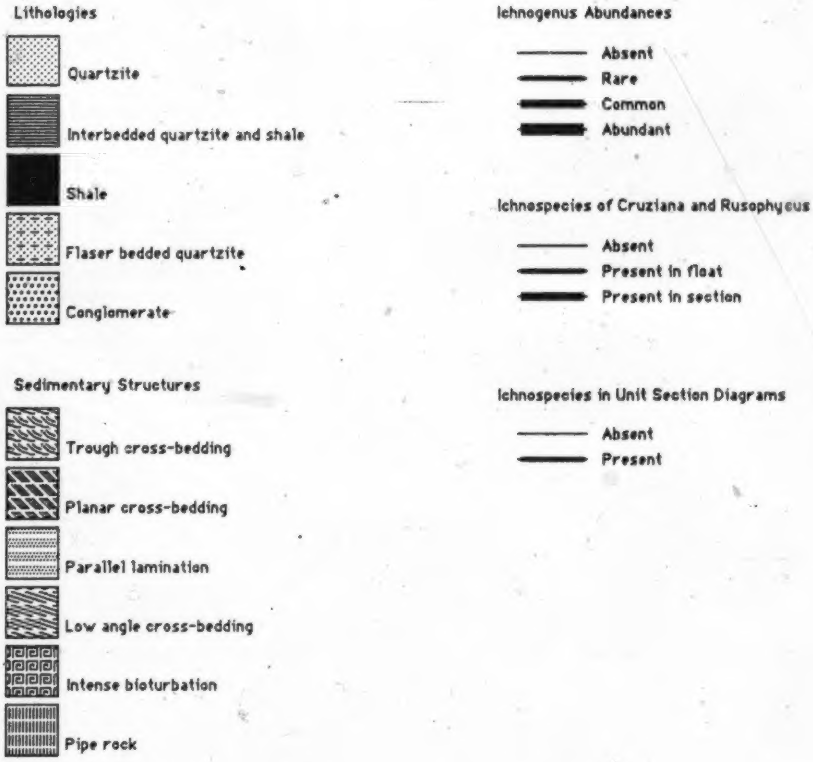

Lithologies
Quartzite
Interbedded quartzite and shale
Shale
Flaser bedded quartzite
Conglomerate
Sedimentary Structures
Trough cross-bedding
Planar cross-bedding
Parallel lamination
Low angle cross-bedding
Intense bioturbation
Pipe rock
Ichnogenus Abundances
Absent
Rare
Common
Abundant
Ichnospecies of Cruziana and Rusophycus
Absent
Present in float
Present in section
Ichnospecies in Unit Section Diagrams
Absent
Present

Figure 14
Key to symbols used in the section diagrams.

Figure 15

Redoubt Mountain section diagram showing the stratigraphic distribution and abundance of ichnogenera by subunit.

Ar=*Arenicolites*; Bg=*Bergaueria*; Ch=*Chondrites*; Co=*Cochlichnus*; Cr=*Cruziana*; Dd=*Didymaulichnus*; Di=*Diplichnites*; Do=*Diplocraterion*; Dp=*Dolopichnus*; Go=*Gordia*; Mo=*Monomorphichnus*; Pa=*Palaeophycus*; Ph=*Phycodes*; Pl=*Planolites*; Pr=*Protichnites*; Py=*Protopaleodictyon*; Rs=*Rusophycus*; Sk=*Skolithos*; Te=*Teichichnus*; Tr=*Trichophycus*; Zo=*Zoophycos*.

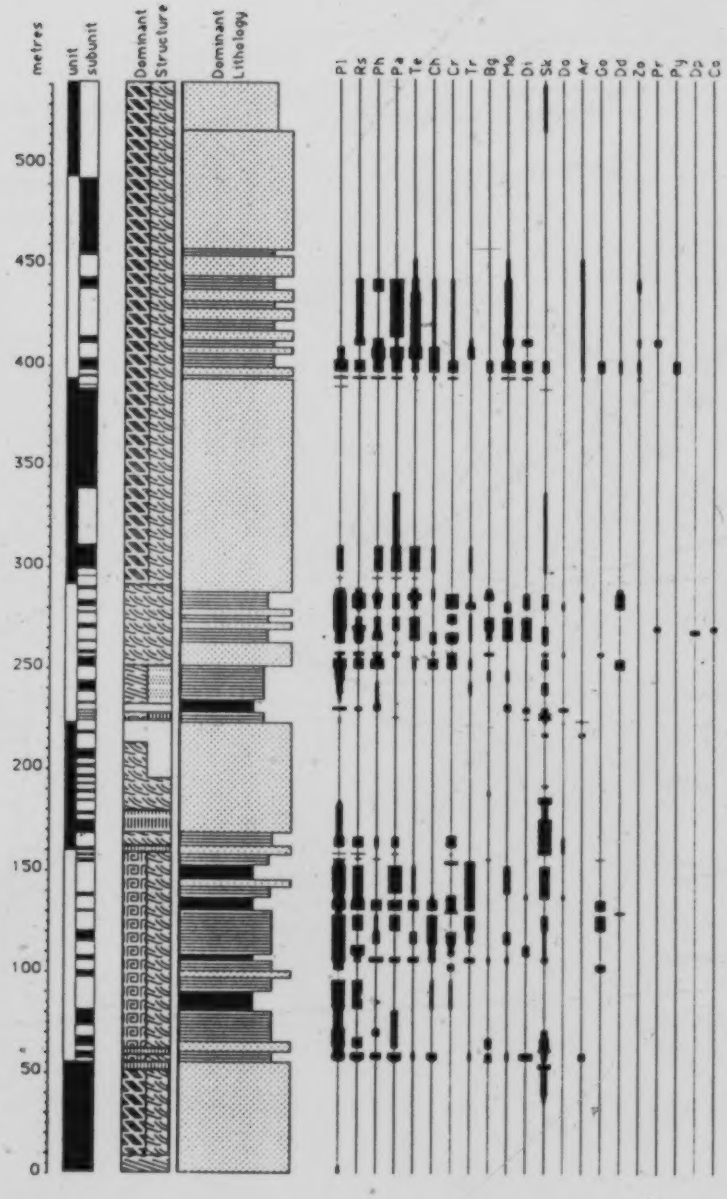
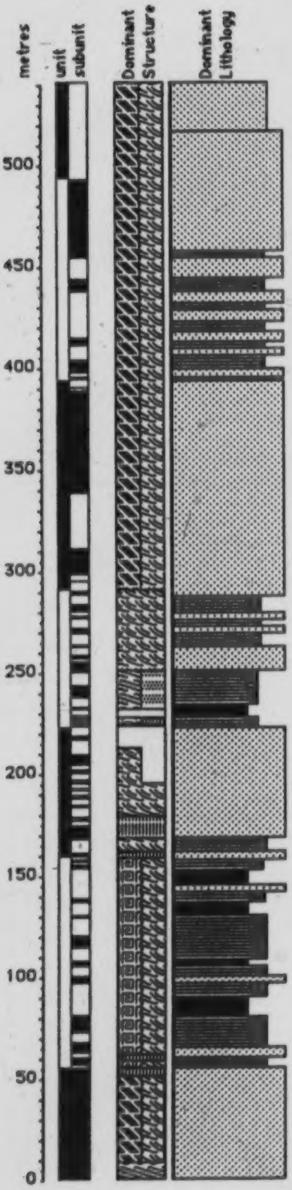

metres
unit
subunit
Dominant Structure
Dominant Lithology
Pl
Rs
Ph
Pa
Te
Ch
Cr
Tr
Bg
Mo
Di
Sk
Do
Ar
Go
Dd
Ze
Pr
Py
Dp
Co
500
450
400
350
300
250
200
150
100
50
0

Figure 16
Redoubt Mountain section diagram with sedimentary descriptions and paleoenvironmental interpretations from Palonen (1976) and Young (1979).



Description and Interpretation

Lenticular quartzite beds made up of lower planar crossbedding and upper trough crossbedding or amalgamated trough cross sets. upper beds are dolomite cemented: Upper tidal flats and migrating tidal channels

Alternating zones of thick, lenticular quartzites with planar and amalgamated trough crossbedding and thinnly interbedded siltstone, sandstone, and silty shale: Upper subtidal to lower intertidal environments

Lenticular quartzite beds made up of lower planar crossbedding and upper trough crossbedding or amaglamated trough cross sets: Upper tidal flats and migrating tidal channels

Interbedded shales and quartzite beds similar to the lower subtidal zone: Subtidal environment

Red and green shales with soft, fissile, red sandstone: Lagoon environment with washover deposits

Upward progression from lenticular beds with lower planar crossbedding and upper trough crossbedding to massive regularly bedded quartzites: Lower tidal flat to backshore deposition

Upward coarsening cycles with increasing frequency and thickness of quartzite beds upward in each cycle: Subtidal environment with cyclical abandonment and infilling of tidal channels

Tangential crossbedding with Skolithos pipe rock: tidal channels and tidal flats

Lenticular bedded with trough and planar crossbeds: Tidal flat with migrating sand bars

Flat to low angle lamination: Swash Zone

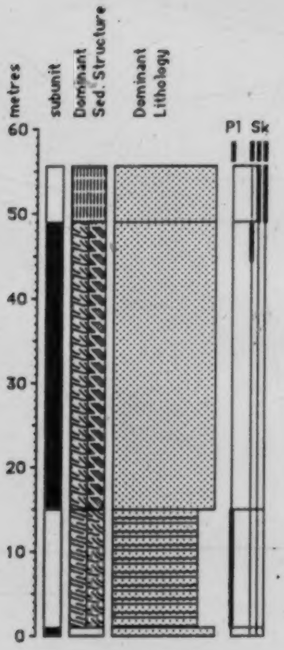

metres
subunit
Dominant Sed. Structure
Dominant Lithology
Pl
Sk
60
50
40
30
20
10
0

Figure 17

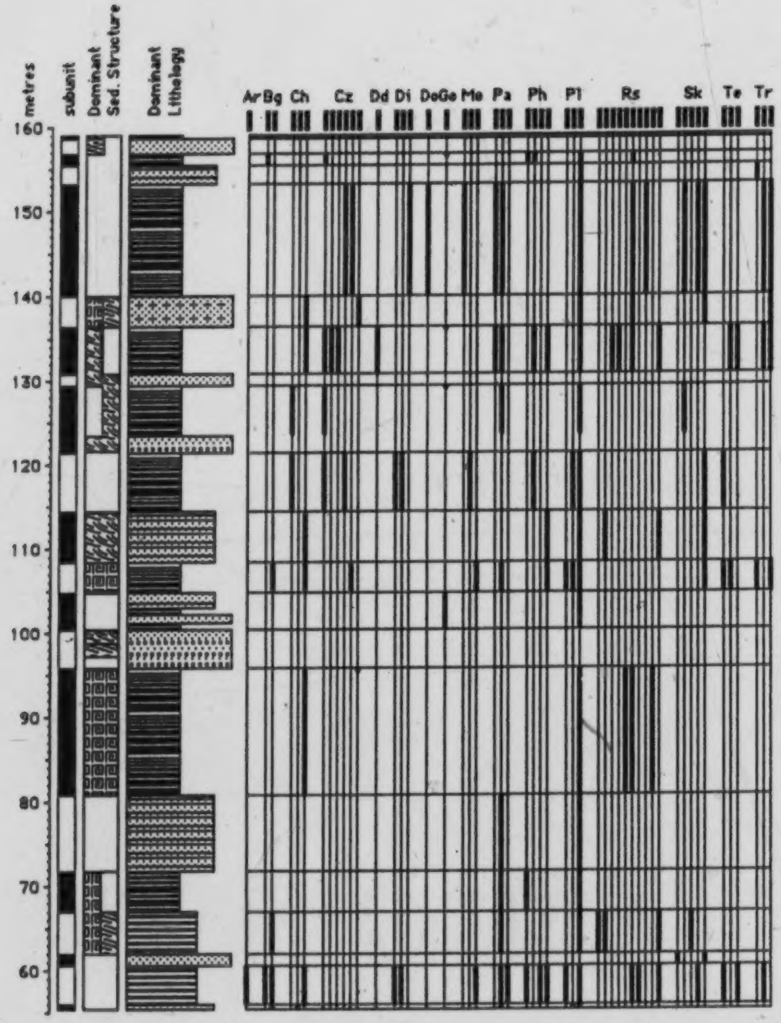
Detailed section diagram of unit 1 showing ichnospecies occurrences. Where more than one ichnospecies of an ichnogenus is present, the different ichnospecies are numbered from left to right on the figure according to the numbering scheme listed below.

Pl1=?*Planolites montanus*; Sk1=*Skolithos linearis* form A; Sk2=*Skolithos linearis* form A, pipe rock; Sk3=*Skolithos linearis* form B

Figure 18

Detailed section diagram of unit 2 showing ichnospecies occurrences. Where more than one ichnospecies of an ichnogenus is present, the different ichnospecies are numbered from left to right on the figure according to the numbering scheme listed below.

Ar1=?*Arenicolites*; Bg1=*Bergaueria perata*; Bg2=?*Bergaueria*; Ch1=*Chondrites* form A; Ch2=*Chondrites* form C; Ch3=*Chondrites* form D; Cz1=*Cruziana semiplicata* form A; Cz2=*Cruziana plicata*; Cz3=*Cruziana* ichnosp. 4; Cz4=*Cruziana problematica* and *Cruziana stromnessa*; Cz5=*Cruziana goldfussi*; Cz6=?*Cruziana*; Dd1=*Didymaulichnus lyelli*; Di1=*Diplichnites* form A; Di2=*Diplichnites* form B; Di3=*Diplichnites* form C; Do1=?*Diplicraterion*; Go1=*Gordia marina*; Mo1=*Monomorphichnus* form B; single scratchmarks; Mo2=*Monomorphichnis* form B; paired scratchmarks; Mo3=?*Monomorphichnus*; Pa1=*Palaeophycus striatus*; Pa2=*Palaeophycus tubularis*; Pa3=?*Palaeophycus*; Ph1=*Phycodes circinatum*; Ph2=*Phycodes palmatum* form A; Ph3=*Phycodes palmatum* form B; Ph4=?*Phycodes*; Pl1=*Planolites annularis*; Pl2=*Planolites beverleyensis*; Pl3=*Planolites montanus*; Rs1=*Rusophycus* ichnosp. 3; Rs2=*Rusophycus rugosa*; Rs3=*Rusophycus avalonensis* form A; Rs4=*Rusophycus avalonensis* form B; Rs5=*Rusophycus ?parallelum*; Rs6=*Rusophycus bilobata* form A; Rs7=*Rusophycus bilobata* form B; Rs8=*Rusophycus eutendorfensis* form A; Rs9=*Rusophycus navicella*; Rs10=?*Rusophycus*; Sk1=*Skolithos* ichnosp. 1; Sk2=*Skolithos* linearis form A; Sk3=*Skolithos* linearis form B, pipe rock; Sk4=*Skolithos* linearis form B; Sk5=possible *Skolithos*; Te1=*Teichichnus rectus* form A; Te2=*Teichichnus rectus* form B; Te3=?*Teichichnus*; Tr1=?*Trichophycus*; Tr2=*Trichophycus venosum*; Tr3=*Trichophycus ?venosum*


metres
subunit
Dominant Sed. Structure
Dominant Lithology
Ar
Bg
Ch
Cz
Dd
Di
DeGe
Me
Pa
Ph
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Sk
Te
Tr
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120
110
100
90
80
70
60

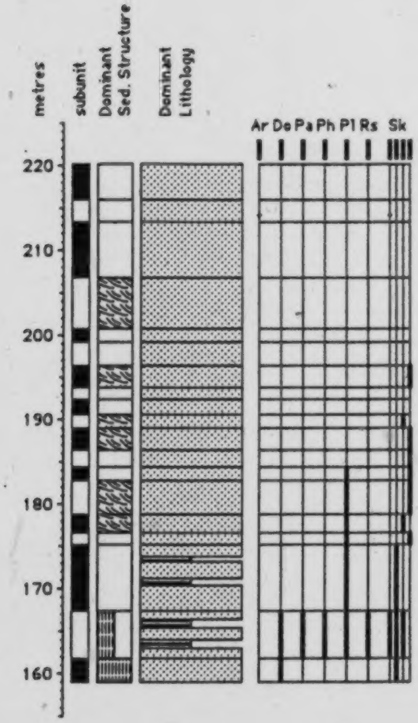


Figure 19

Detailed section diagram of unit 3 showing ichnospecies occurrences. Where more than one ichnospecies of an ichnogenus is present, the different ichnospecies are numbered from left to right on the figure according to the numbering scheme listed below.

Ar1=*Arenicolites* ichnosp.; Do1=?*Diplocraterion*; Pa1=*Palaeophycus tubularis*; Ph1=?*Phycodes*; Pl1=*Planolites montanus*; Rs1=*Rusophycus bilobata*; Sk1=*Skolithos linearis* form A, pipe rock; Sk2=*Skolithos linearis* form B, pipe rock; Sk3=*Skolithos linearis* form B; Sk4=possible *Skolithos*

Figure 20

Detailed section diagram of unit 4 showing ichnospecies occurrences. Where more than one ichnospecies of an ichnogenus is present, the different ichnospecies are numbered from left to right on the figure according to the numbering scheme listed below.

Ar1=*Arenicolites* ichnosp.; Ar2=?*Arenicolites*; Bg1=*Bergaueria hemispherica*; isolated; Bg2=*Bergaueria hemispherica*; close packed; Bg3=*Bergaueria perata*; Bg4=?*Bergaueria*; Ch1=*Chondrites* form A; Ch2=*Chondrites* form B; Ch3=*Chondrites* form D; Ch4=?*Chondrites*; Co1=*Cochlichnus* ichnosp.; Cz1=*Cruziana semiplicata* form B; Cz2=*Cruziana plicata*; Cz3=*Cruziana* ichnosp. 2 form A; Cz4=*Cruziana* ichnosp. 2 Form B; Cz5=*Cruziana* ichnosp. 4; Cz6=*Cruziana pormensis*; Cz7=*Cruziana problematica* and *Cruziana stromnessa*; Cz8=*Cruziana* ichnosp. 1; Cz9=*Cruziana clavata*; Cz10=?*Cruziana*; Dd1=*Didymaulichnus lyelli* (5mm); Dd2=*Didymaulichnus lyelli* (10mm); Dd3=?*Didymaulichnus*; Di1=*Diplichnites* form A; Di2=*Diplichnites* form C; Di3=*Diplichnites* form D; Do1=?*Diplocraterion*; Do2=*Diplocraterion* ichnosp.; Dp1=*Dolopichnus* ichnosp.; Go1=*Gordia marina*; Mo1=*Monomorphichnus* form A; Mo2=*Monomorphichnus* form B; Mo3=?*Monomorphichnus*; Pa1=*Palaeophycus herberti*; Pa2=*Palaeophycus striatus*; Pa3=possible *Palaeophycus*; Ph1=*Phycodes palmatum* form A; Ph2=*Phycodes palmatum* form B; Ph3=*Phycodes flabellum*; Ph4=?*Phycodes*; Pl1=*Planolites annulatus*; Pl2=*Planolites beverleyensis*; Pl3=*Planolites montanus*; Pr1=?*Protichnites*; Rs1=*Rusophycus* ichnosp. 3; Rs2=*Rusophycus carinatus*; Rs3=*Rusophycus bilobata* form A; Rs4=*Rusophycus bilobata* form B; Rs5=*Rusophycus eutendorfensis* form B; Rs6=*Rusophycus* ichnosp. 2; Rs7=?*Rusophycus*; Sk1=*Skolithos linearis* form A, pipe rock; Sk2=*Skolithos linearis* form A; Sk3=*Skolithos linearis* form B, pipe rock; Sk4=?*Skolithos*; Te1=*Teichichnus rectus* form A; Te2=*Teichichnus rectus* form B; Te3=*Teichichnus stellatus*; Te4=?*Teichichnus*; Tr1=*Trichophycus venosum*; Tr2=*Trichophycus ?venosum*; Tr3=?*Trichophycus*

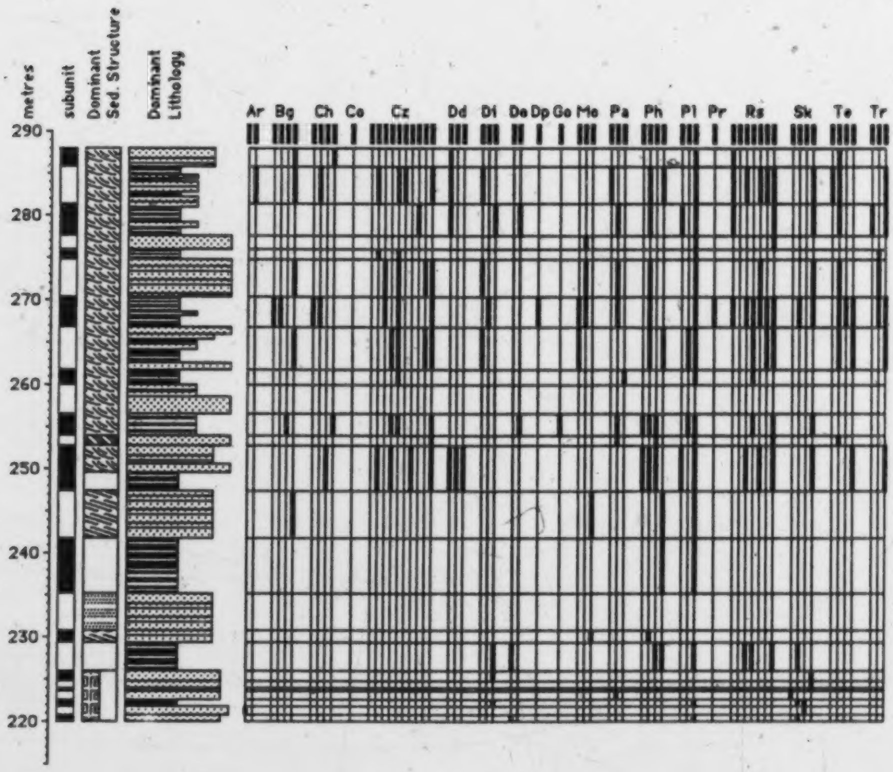

metres
subunit
Dominant Sed. Structure
Dominant Lithology
290
280
270
260
250
240
230
220
Ar
Bg
Ch
Co
Cz
Dd
Di
Do
Dp
Go
Mo
Pa
Ph
Pl
Pr
Rs
Sk
Te
Tr

Figure 21

Detailed section diagram of unit 5 showing ichnospecies occurrences. Where more than one ichnospecies of an ichnogenus is present, the different ichnospecies are numbered from left to right on the figure according to the numbering scheme listed below.

Ch1=*Chondrites* form A; Mo1=?*Monomorphichnus*; Pa1=*Palaeophycus striatus*; Pa2=*Palaeophycus tubularis*; Pa3=?*Palaeophycus*; Ph1=*Phycodes circinatum*; Ph2=*Phycodes palmatum* form A; Ph3=*Phycodes palmatum* form B; Ph4=?*Phycodes*; Pl1=*Planolites annulatus*; Pl2=*Planolites montanus*; Sk1=*Skolithos* ichnosp. 1; Sk2=*Skolithos linearis* form B; Sk3=possible *Skolithos*; Te1=*Teichichnus rectus* form A; Te2=*Teichichnus rectus* form B; Te3=*Teichichnus rectus* form C; Te4=?*Teichichnus*; Tr1=*Trichophycus venosum*; Tr2=*Trichophycus* ?*venosum*

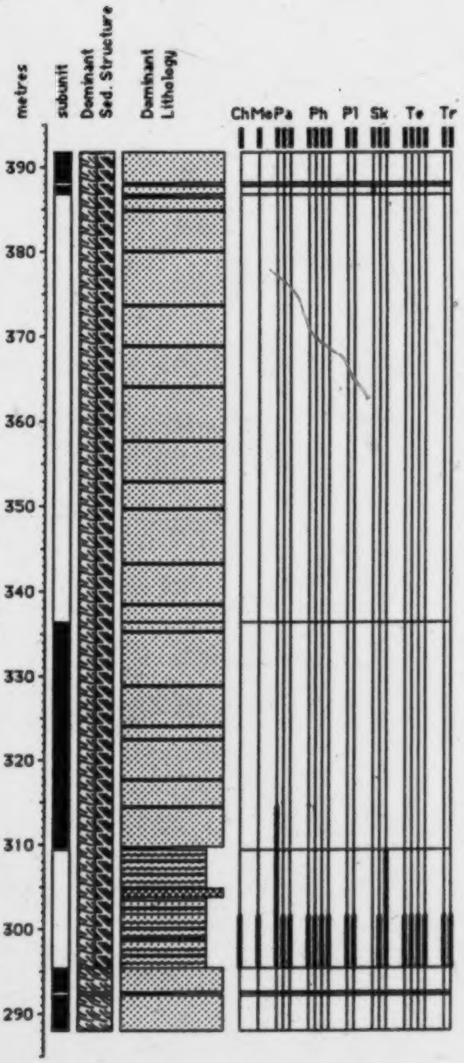

metres
subunit
Dominant Sed. Structure
Dominant Lithology
Ch
Me
Pa
Ph
Pl
Sk
Te
Tr
390
380
370
360
350
340
330
320
310
300
290

Figure 22

Detailed section diagram of unit 6 showing ichnospecies occurrences. Where more than one ichnospecies of an ichnogenus is present, the different ichnospecies are numbered from left to right on the figure according to the numbering scheme listed below.

Ar1=?*Arenicolites*; Bg1=*Bergaueria hemispherica*; Bg2=?*Bergaueria*; Ch1=*Chondrites* form A; Ch2=*Chondrites* form B; Ch3=*Chondrites* form D; Cz1=*Cruziana arizonensis*; Cz2=*Cruziana plicata*; Cz3=*Cruziana* ichnosp. 2 form A; Cz4=*Cruziana* ichnosp. 2 form B; Cz5=*Cruziana* ichnosp. 4; Cz6=*Cruziana stromnesa*; Cz7=*Cruziana clavata*; Cz8=?*Cruziana*; Dd1=*Didymaulichnus lyelli*; Di1=*Diplichnites* form A; Di2=*Diplichnites* form B; Di3=*Diplichnites* form C; Di4=*Diplichnites* form E; Di5=?*Diplichnites*; Go1=*Gordia marina*; Mo1=*Monomorphichnus* form A; Mo2=*Monomorphichnus* form B; Mo3=?*Monomorphichnus*; Pa1=*Palaeophycus striatus*; Pa2=*Palaeophycus tubularis*; Pa3=?*Palaeophycus*; Ph1=*Phycodes circinatum*; Ph2=*Phycodes palmatum* form A; Ph3=*Phycodes palmatum* form B; Ph4=*Phycodes ?flabellum*; Ph5=?*Phycodes*; Pl1=*Planolites annulatus*; Pl2=*Planolites beverleyensis*; Pl3=*Planolites montanus*; Pr1=*Protichnites* ichnosp.; Py1=*Protopaleodictyon* ichnosp.; Rs1=*Rusophycus* ichnosp. 3; Rs2=*Rusophycus* ichnosp. 1; Rs3=*Rusophycus rugosa*; Rs4=*Rusophycus bilobata* form A; Rs5=*Rusophycus cerecedensis*; Rs6=*Rusophycus eutendorfensis* form A; Rs7=*Rusophycus eutendorfensis* form B; Rs8=*Rusophycus* ichnosp. 2; Rs9=*Rusophycus navicella*; Rs10=?*Rusophycus*; Sk1=*Skolithos linearis* form A; Sk2=*Skolithos linearis* form B; Sk3=possible *Skolithos*; Te1=*Teichichnus rectus* form A; Te2=*Teichichnus rectus* form B; Te3=*Teichichnus rectus* form C; Te4=*Trichophycus stellatus*; Te5=?*Teichichnus*; Tr1=*Trichophycus venosum*; Zo1=*Zoophycos* ichnosp.

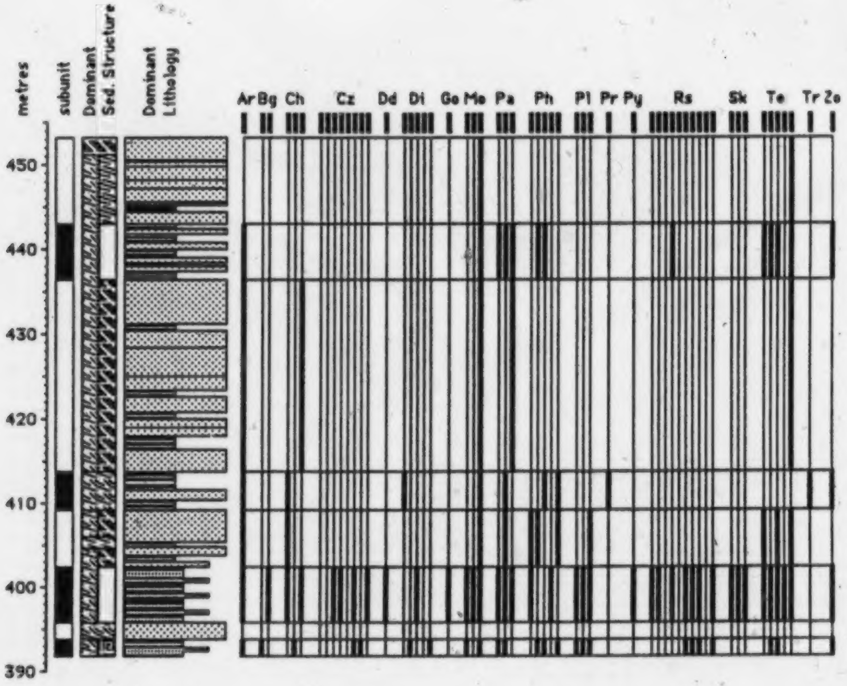

metres
subunit
Dominant Sed. Structure
Dominant Lithology
Ar
Bg
Ch
Cz
Dd
Di
Ge
Mo
Pa
Ph
Pl
Pr
Py
Rs
Sk
Te
Tr
Zo
450
440
430
420
410
400
390

Figure 23

Redoubt Mountain section diagram showing the stratigraphic distribution of ichnospecies of *Cruziana* and *Rusophycus* in this study.

AR=*arizonensis*; AVa=*avalonensis* form A; AVb=*avalonensis* form B; BLa=*bilobatum* form A; BLb=*bilobatum* form B; CA=*carinatus*; CE=*cerecedensis*; CL=*clavata*; EUa=*eutendorfensis* form A; EUb=*eutendorfensis* form B; GO=*goldfussi*; I1=ichnosp. 1; I2=ichnosp. 2; I2a=ichnosp. 2 form A; I2b=ichnosp. 2 form B; I3=ichnosp. 3; I4=ichnosp. 4; NA=*navicella*; PA=*parallelum*; PL=*plicata*; PR=*pormensis*; RG=*rugosa*; SEa=*semiplicata* form A; SEb=*semiplicata* form B; SP=*stromnessa* and *problematica*; ?=identified to ichnogeneric level only.

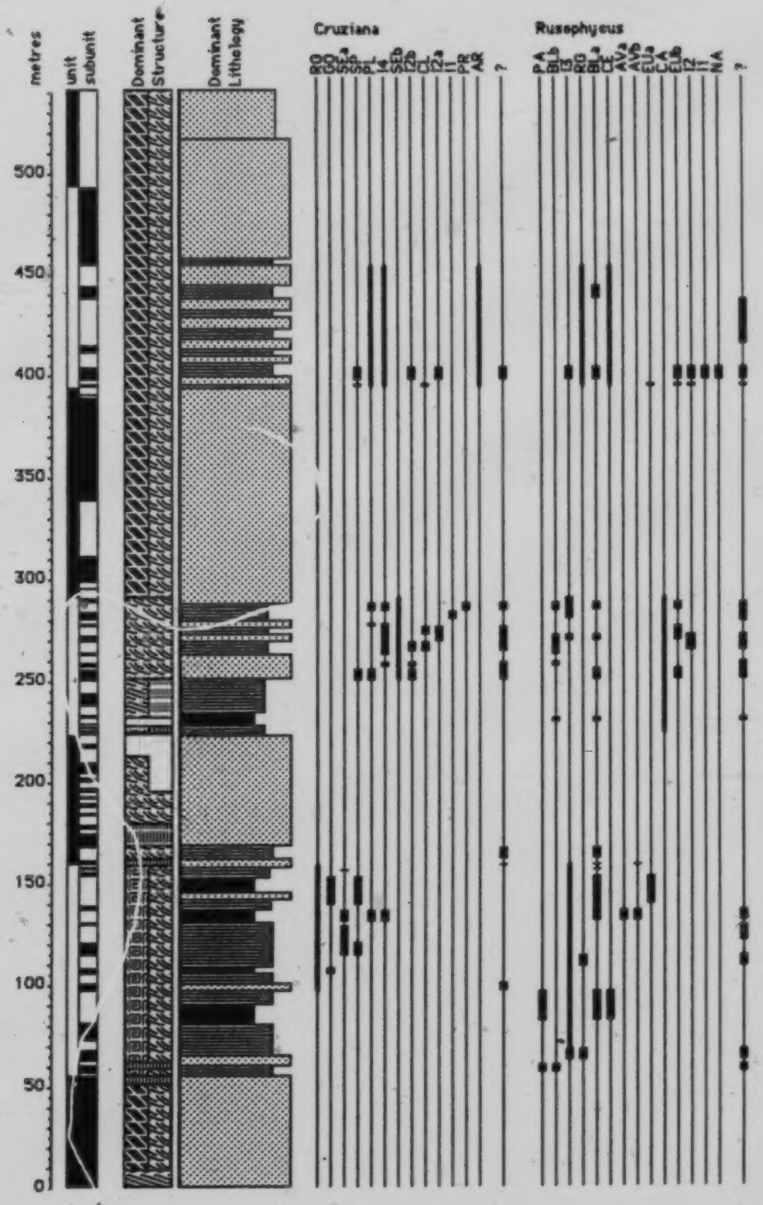

metres
unit
subunit
Dominant Structure
Dominant Lithology
Cruziana
RO
GO
SEa
SEb
PL
I4
SEb
I2b
CL
I2a
I1
PR
AR
?
Rusophycus
PA
BLb
IS
RO
BLa
CE
AVa
AVb
EUa
CA
EUb
I2
I1
NA
?
0
50
100
150
200
250
300
350
400
450
500

Figure 24

Known stratigraphic distribution of arthropod generated ichnogenera and ichnospecies of *Cruziana*, not including data from this study.

*C. clavata includes C. subangulatum (Osgood, 1970).

Data from Crimes (1970a, 1970b, 1970c, 1975a, 1975c), Osgood (1970), Seilacher (1970), Young (1972), Häntzschel (1975), Osgood and Drennen (1975), Alpert (1976), Bergström (1976), Crimes and Marcos (1976), Baldwin (1977a), Crimes *et al.* (1977), Bromley and Asgaard (1979), Shone (1979), Bradshaw (1981), Fillion and Pickerill (1984), Crimes and Anderson (1985), Pienkowski (1985), Landing and Brett (1987).

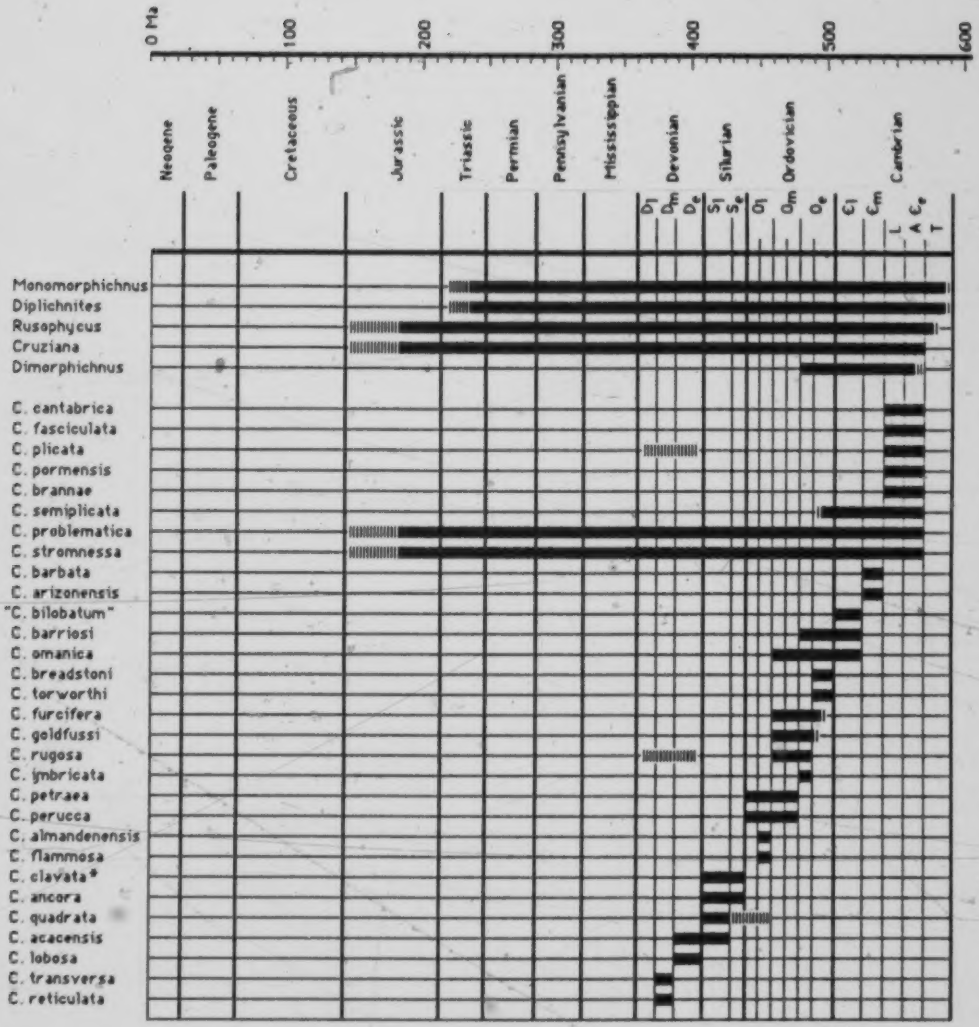
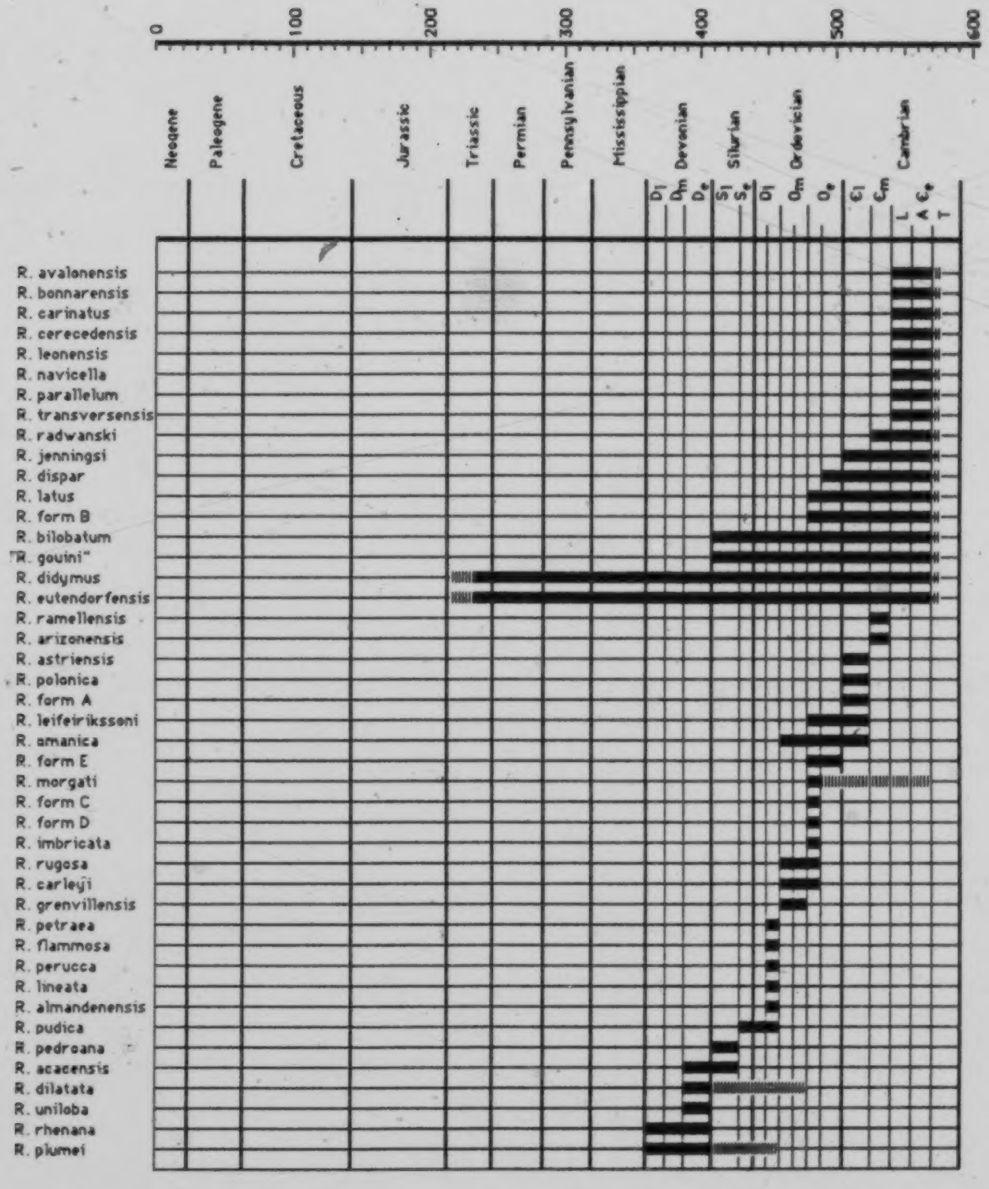

0 Ma
100
200
300
400
500
600
Neogene
Paleogene
Cretaceous
Jurassic
Triassic
Permian
Pennsylvanian
Mississippian
Devonian
Silurian
Ordovician
Cambrian
D_l
D_m
D_e
S_l
S_e
O_l
O_m
O_e
$Є_l$
$Є_m$
L
A
$Є_e$
T
Monomorphichnus
Diplichnites
Rusophycus
Cruziana
Dimorphichnus
C. cantabrica
C. fasciculata
C. plicata
C. pormensis
C. brannae
C. semiplicata
C. problematica
C. stromnessa
C. barbata
C. arizonensis
"C. bilobatum"
C. barriosi
C. omanica
C. breadstoni
C. torworthi
C. furcifera
C. goldfussi
C. rugosa
C. imbricata
C. petraea
C. perucca
C. almandenensis
C. flammosa
C. clavata*
C. ancora
C. quadrata
C. acacensis
C. lobosa
C. transversa
C. reticulata

Figure 25

Known stratigraphic distribution of ichnospecies of *Rusophycus*, not including data from this study.

Data from Crimes (1970a, 1970b, 1970c, 1975a, 1975c), Osgood (1970), Seilacher (1970), Young (1972), Häntzschel (1975), Osgood and Drennen (1975), Alpert (1976), Bergström (1976), Crimes and Marcos (1976), Baldwin (1977a), Crimes *et al.* (1977), Bromley and Asgaard (1979), Shone (1979), Bradshaw (1981), Fillion and Pickerill (1984), Crimes and Anderson (1985), Pienkowski (1985), Landing and Brett (1987).


0
100
200
300
400
500
600
Neogene
Paleogene
Cretaceous
Jurassic
Triassic
Permian
Pennsylvanian
Mississippian
Devonian
Silurian
Ordovician
Cambrian
D$_l$
D$_m$
D$_e$
S$_l$
S$_e$
O$_l$
O$_m$
O$_e$
Є$_l$
Є$_m$
L
A
Є$_e$
T
R. avalonensis
R. bonnarensis
R. carinatus
R. cerecedensis
R. leonensis
R. navicella
R. parallelum
R. transversensis
R. radwanski
R. jenningsi
R. dispar
R. latus
R. form B
R. bilobatum
"R. gouini"
R. didymus
R. eutendorfensis
R. ramellensis
R. arizonensis
R. astriensis
R. polonica
R. form A
R. leifeiriksson
R. amanica
R. form E
R. morgati
R. form C
R. form D
R. imbricata
R. rugosa
R. carleyi
R. grenvillensis
R. petraea
R. flammosa
R. perucca
R. lineata
R. almandenensis
R. pudica
R. pedroana
R. acacensis
R. dilatata
R. uniloba
R. rhenana
R. plumei

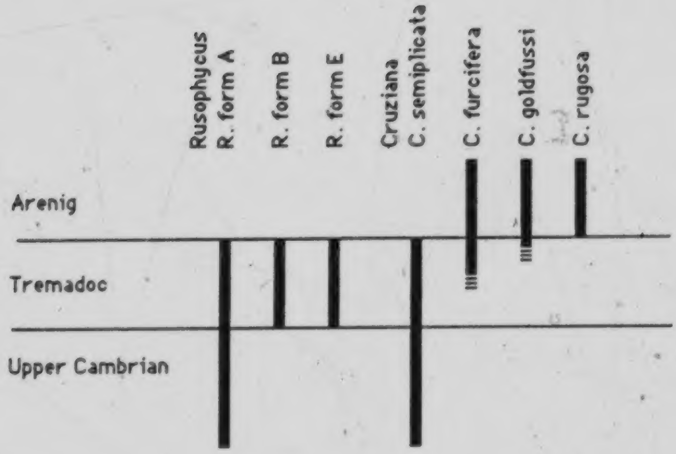


Figure 26

The distribution of Upper Cambrian-Lower Ordovician index ichnofossils across the Cambrian-Ordovician boundary in Europe and Newfoundland.

Modified from Crimes (1969, 1975a, 1975c); Baldwin (1977a); and Pickerill *et al.* (1984)

Figure 27

Comparison of the stratigraphic ranges in the literature for ichnospecies of *Cruziana* and *Rusophycus* occurring in the Gog Group at Lake Louise with their chronostratigraphic position in the Gog Group. Stratigraphic ranges from the literature are show as solid and dashed bars. The approximate age of the Gog Group is shown as a shaded zone down the left hand side of the diagram.

Data from Bergström (1970, 1976), Seilacher (1970), Osgood and Drennen (1975), Baldwin (1977a), Crimes *et al.* (1977), Bromley and Asgaard (1979), Bradshaw (1981).

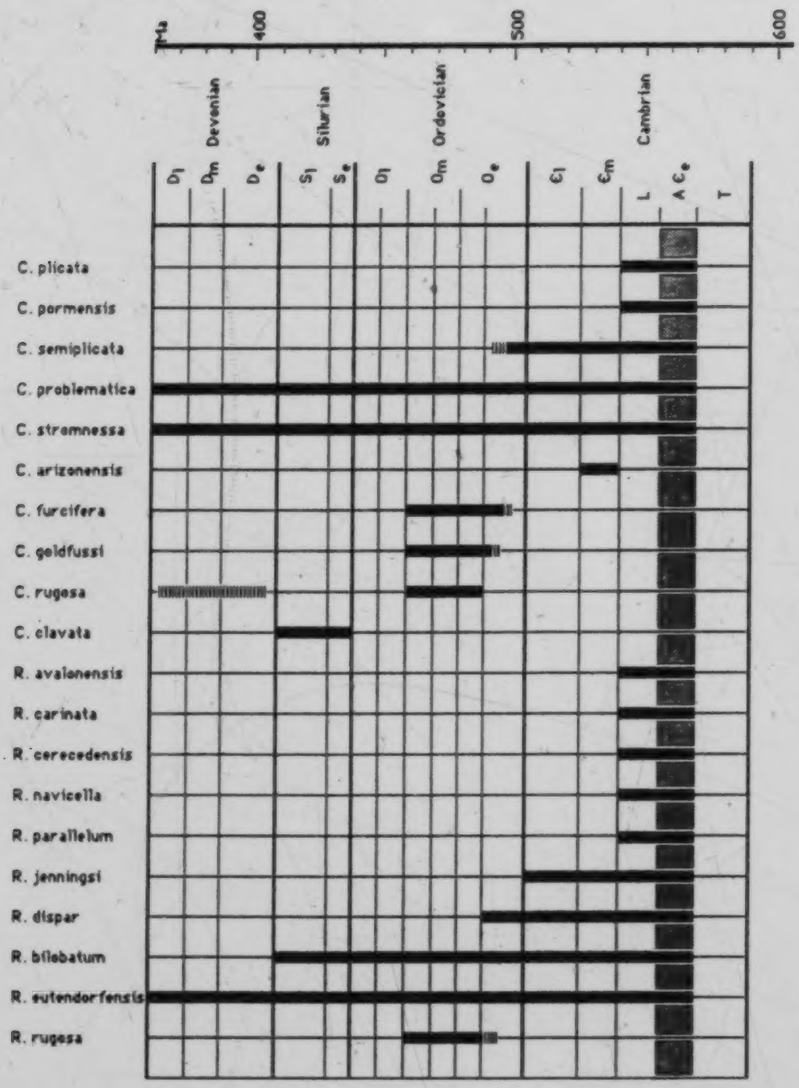

Ma
400
500
600
Devonian
Silurian
Ordovician
Cambrian
Dl
Dm
De
Sl
Se
Ol
Om
Oe
Єl
Єm
L
A Єe
T
C. plicata
C. pormensis
C. semiplicata
C. problematica
C. stromnessa
C. arizonensis
C. furcifera
C. goldfussi
C. rugosa
C. clavata
R. avalonensis
R. carinata
R. cerecedensis
R. navicella
R. parallelum
R. jenningsi
R. dispar
R. bilobatum
R. eutendorfensis
R. rugosa

Figure 28

Stratigraphic distribution of trace fossils and selected body fossils across the Precambrian-Cambrian boundary.

Modified from Crimes (1987), McMenamin (1987), Narbonne *et al.* (1987), Esakova (1988).

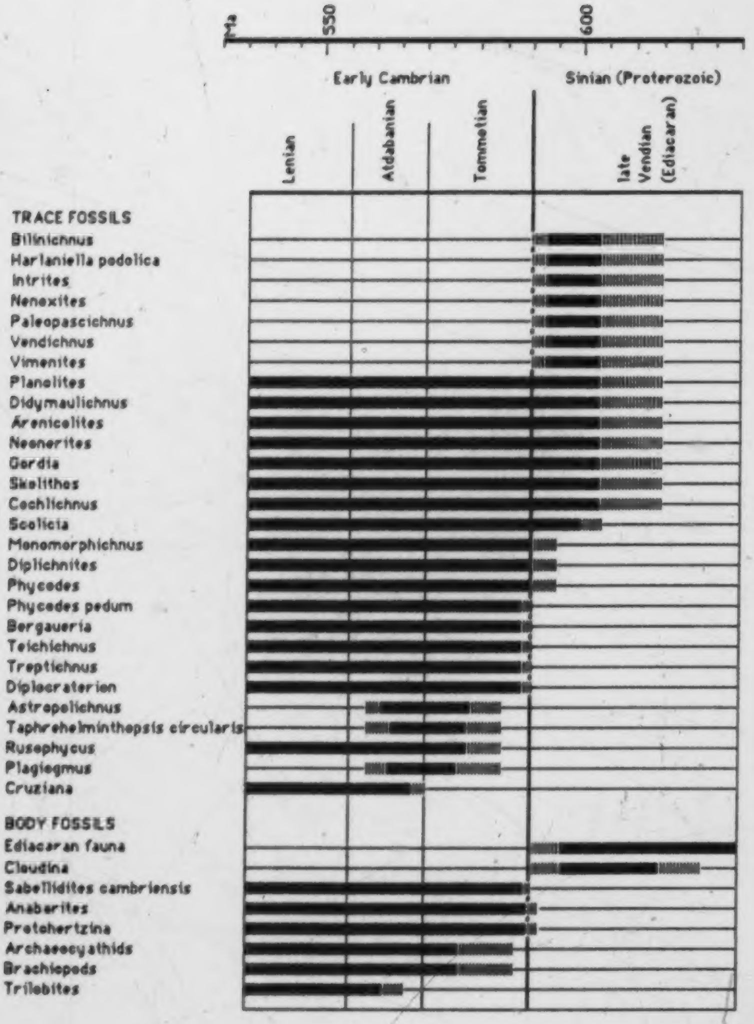

Ma
550
600
Early Cambrian
Sinian (Proterozoic)
Lenian
Atdabanian
Tommotian
late Vendian (Ediacaran)
TRACE FOSSILS
Bilinichnus
Harlaniella podolica
Intrites
Nenoxites
Paleopascichnus
Vendichnus
Vimenites
Planolites
Didymaulichnus
Arenicolites
Neonerites
Gordia
Skolithos
Cochlichnus
Scolicia
Monomorphichnus
Diplichnites
Phycodes
Phycodes pedum
Bergaueria
Teichichnus
Treptichnus
Diplocraterion
Astropolichnus
Taphrohelminthopsis circularis
Rusophycus
Plagiogmus
Cruziana
BODY FOSSILS
Ediacaran fauna
Cloudina
Sabelliditès cambriensis
Anabarites
Protohertzina
Archaeocyathids
Brachiopods
Trilobites

Plate 1

Redoubt Mountain section photographs, 1.2 m field assistant for scale.

1a; the south face of Redoubt Mountain showing the alternating resistant and recessive units. The basal cliff forming unit is a conglomeratic sandstone near the top of the Miette Group (Hector Formation). The second, third, and fourth cliff forming units comprise units 1, 3, and 5 respectively, of the Gog Group. Unit 6 grades into unit 7 below the deeply runneled, smooth surfaced cliff at the top of the mountain. This upper most cliff and the recessive shales below comprise the Mount Whyte Formation. The thickness of the Gog Group at Redoubt Mountain is 540 m. 1b; the avalanche chute to the left of 1a, in which most of the collecting and section measuring was done. The photo extends from unit 1 of the Gog Group to the base of the Mount Whyte Formation cliff. Collecting in unit 4 was done in another chute at the far right of 1a. 1c; the unconformable contact, in the chute from 1b, between the slates of the Miette Group and the basal conglomeratic orthoquartzite of the Gog Group. 1d; a typical coarsening upward cycle from unit 2, zone 2.

Plate 2

Miscellaneous sedimentary features at Redoubt Mountain.

2a; wavy bedded thin quartzite and shale laminae from unit 2, zone 2 coarsening upward cycles. 2b; herringbone planar cross stratification from float at Moraine Lake. 2c; wavy bedded and linsen bedded quartzite and shale laminae from unit 2, zone 2 coarsening upward cycles. 2d; low angle to flat laminated soft sandstones from subunit 6d. 2e; the transition from the soft, pale green mottled sandstones of subunit 4a to the well indurated, pink quartzite of subunit 4b. 2f; *Rusophycus* ichnosp. preserved as a quartzite infilled cast within thinly interbedded quartzite and shale.

scale bar = 5 cm

Plate 3

Physical bedding surface features.

3a; descication mud cracks on the base of a thick cross-bedded quartzite float block at Lake O'Hara. 3b; synaeresis mud cracks in wavy to flaser bedded thin quartzite and shale lamina, from unit 2. 3c; descication mud cracks on the base of a thick cross-bedded quartzite overlying a thin grey shale, near the base of unit 1. 3d; mud cracks on the base of a thick, cross-bedded quartzite float block at Moraine Lake. 3e; lunate ripple bed forms on a quartzite float block with vague cross-bedding, within unit 4. 3f; shrinkage cracks in a gritty shale float block at Moraine Lake.

scale bar = 5 cm

Plate 4

Physical, upper bedding surface features.

4a; upper right corner: cast of surface run-off marks on the base of a thin, silty sandstone lamina in subunit 6a. Lower left corner shows a *Monomorphichnus* form B. 4b; shallow water interference ripples on the upper surface of a thin silty sandstone lamina from unit 4, zone 2. 4c; planed off symmetrical ripples on the upper surface of a thin quartzite bed from near the top of the upper most coarsening upward cycle in unit 2, zone 2. 4d; shallow water interference ripples on the upper surface of a thin, lenticular quartzite bed from the same stratigraphic interval as 4c. 4e; wind adhesion ripples on the upper surface of a thin, soft sandstone bed from unit 4, zone 2. 4f; the basal surface of the sample in 4d showing a number of small *Rusophycus* ichnosp. 3.

scale bar = 2 cm

Plate 5

Miscellaneous physical sedimentary features.

5a; a large load cast at the base of one of the thick resistant subunits in unit 6. 5b; large scale planar cross-bedding in thick, lenticular quartzite beds in a resistant subunit in unit 6. 5c; side section of one of the thin clast supported conglomerate beds in unit 5 showing the well rounded quartzose pebbles in a pelitic matrix. 5d; a typical basal bedding surface in subunit 6a showing small *Rusophycus eutendorfensis*, *Planolites*, and fine linear scour marks. 5e; amalgamated trough and low angle cross-bedding in a thin quartzite bed from a resistant subunit in unit 6. 5f; an example of the unusual pitted bedding surfaces from thick quartzite beds in unit 2, probably representing cavities left by conglomerate pebbles that have come loose.

scale bars: 10 cm 5a 5b; 2 cm 5c, 5d, 5f; 15 cm 5e

Plate 6

Bergaueria.

6a; apical view of a *Bergaueria perata* showing a flat apical surface with concentric, circular runnels. 6b; side view of a tilted *Bergaueria perata* showing the concentric ridges down the side of the trace fossil. 6c; side view of *Bergaueria perata* with faint, fine radial ridges. 6d; apical view of a *Bergaueria radiata* showing the apical mound with wide, well spaced radial ridges. 6e; apical view of a *Bergaueria perata* with a central apical button. 6f; apical view of the sample in 6d with a specimen of *Bergaueria hemispherica* (upper right), *Bergaueria perata* (lower left), and *Bergaueria radiata* (lower right).

scale bar = 1 cm

Plate 7

Bergaueria and *Dolopichnus* clusters.

7a; a dense cluster of *Bergaueria hemispherica* showing the range from straight specimens within the cluster to slanted specimens on its periphery. 7b; a close up of the slanted *Bergaueria hemispherica* from 7a and *Chondrites* form C between the *Bergaueria* specimens. 7c; a float block from Moraine Lake showing two distinct size classes of *Bergaueria hemispherica* with abundant *Chondrites* form C in the intervening spaces. 7d; *Dolopichnus* on the base of a thick quartzite bed with flecks of the grey shale which originally surrounded the burrows. 7e; close up apical view of *Dolopichnus* from the float block in 7f. 7f; a dense cluster of *Dolopichnus* on the base of a thin float block in unit 4.

scale bar = 5 cm

Plate 8

Chondrites.

8a; *Chondrites* form B burrows on the outer surface of a *Teichichnus rectus*. 8b; *Chondrites* form D showing a number of branches off a continuous main tunnel. 8c; a typical dense assemblage of *Chondrites* form C on the base of a thick quartzite bed. 8d; an example of the typical aspect of *Chondrites* form B. Actual branching is rarely observed, however, the general pattern is suggestive of *Chondrites* rather than *Planolites*. 8e; a dense assemblage of short, narrow burrows suggestive of *Chondrites* form B, on the base of a thin sandstone bed. 8f; *Chondrites* form A showing an irregular, radiating branching pattern.

scale bar = 2 cm

Plate 9

Palaeophycus and *Planolites*.

9a; *Palaeophycus tubularis*. The arrowed specimen shows the thin black lining. The tapering is caused by the vertical curvature of the specimen. 9b; *Palaeophycus striatus* showing the long, fine, single striae; differing from the short anastomosing scratch marks of *Trichophycus*. 9c; a transverse view of *Palaeophycus heberti* showing the diagnostic thick lining. The white colour of the lining may be due to organic compounds in the lining (mucus) effecting the rock's diagenesis. 9d; *Planolites montanus* in a dense, intertwining assemblage. 9e; *Planolites annularis* (arrowed) showing more or less regular annular rings. 9f; *Planolites beverleyensis* in a dense, intertwining assemblage.

scale bar = 2 cm

Plate 10

Miscellaneous ichnogenera.

10a; *Protichnites* ichnosp. showing a compound appendage imprint: a proximal simple , more or less circular impression (single arrow), and a distal elongate impression made up of a number of short, parallel striations (double arrow). This track must have been made by an animal with a compound appendage structure consisting of an outer spinose branch and an inner simple branch; similar to the exite and telopodite of trilobites. 10b; *Protopaleodictyon*, a horizontal, meandering burrow system with frequent, short side branches. 10c; *Zoophycos* spreiten (arrowed). 10d; *Gordia marina* on the base of a thick quartzite bed and showing the typical irregular looping and level overcrossing. 10e; *Protichnites* ichnosp. consisting of simple imprints indicating that little or no slippage occurred between the appendages and the substrate. 10f; *Cochlichnus* showing the smooth but abrupt changes in direction.

scale bar = 1 cm

Plate 11

Skolithos.

11a; close up of the basal surface of a thick, quartzite bed made up of *Skolithos linearis* form B pipe rock. 11b; distance view of *Skolithos linearis* form B pipe rock form 11a, subunit 3a. 11c; *Skolithos linearis* form B showing peripheral weathered out zones around the shafts, suggesting the presence of a lining. 11d; side section of the *Skolithos linearis* form B pipe rock from 11b, showing the abundant shale flasers and the rather low density of visible shafts compared to the transverse sections. 11e; transverse view of *Skolithos linearis* form A pipe rock, showing how difficult it can be to see shafts without a contrasting lining. 11f; *Skolithos linearis* form B shoving distinct dark linings.

scale bar = 2 cm

Plate 12

Shafts.

12a; transverse view of ?*Palaeophycus* showing the two differentially coloured halos in the surrounding substrate. 12b; *Skolithos* ichnosp. 1 from unit 5 with the typically dark infill and funnel-shaped tops. The amalgamated trough cross-bedding and multiple reactivation surfaces are one of the typical cross-bedding styles in unit 5. 12c; side view of ?*Palaeophycus* from 12a showing the small bends and fine peristaltic-like annulations. 12d; *Skolithos annulatus* in a *Skolithos linearis* pipe rock. 12e; a shale infilled *Diplocraterion parallelum* in a clean quartzite matrix. Spreiten show up as broadly concave-up dark bands between the tube arms. 12f; *Arenicolites* ichnosp. consisting of simple U-shaped burrows infilled with loose sandstone, within a well indurated quartzite.

scale bar = 1 cm

Plate 13

Phycodes.

13a; *Phycodes flabellum*, of a tight bundle of overlapping tubes. 13b; ?*Phycodes*, a wide fan-shaped burrow made up of a number of longitudinal spreiten. 13c; *Phycodes palmatum* form A. 13d; *Phycodes palmatum* form A. 13e; an exceptionally large *Phycodes palmatum* form B.

scale bar = 2 cm

Plate 14

Phycodes and *Teichichnus*.

14a; *Teichichnus ?stellatus* from the large slab in 21a. 14b; *Teichichnus rectus* form B showing distinct gaps between the spreiten. 14c; *Phycodes circinatum* showing one long tube and a tight fan of tubes below. 14d; *Phycodes circinatum* from 14c; showing the transverse section with vague circles representing the branches of the burrow system. 14e; *Phycodes ?flabellum*, a circular burrow that widens markedly in one direction, through a number of overlapping branches.

scale bar = 1 cm

Plate 15

Teichichnus.

15a; *Teichichnus rectus* form C. 15b; *Teichichnus ?stellatus*. 15c,d; two views of *Teichichnus rectus* form A. 15e; an exceptionally large *Teichichnus rectus* form C showing the characteristic concave up curve. 15f; an isolated spreiten from *Teichichnus rectus* form B showing the extreme length and the fact that spreiten are separated by distinct zones of weathered out material.

scale bar = 1 cm

Plate 16

Trichophycus.

16a; *Trichophycus venosum* with periodic constrictions and randomly oriented anastomosing striations. 16b; basal view of *Trichophycus venosum* showing the finely paired, anastomosing striations. 16c; basal view of a ?*Trichophycus venosum* showing irregular transverse scratch marks. 16d; transverse view of a ?*Trichophycus venosum* projecting from a thin interlaminated sandstone and shale layer in unit 2, note the quartzite infill with thin shale laminae. 16e; long specimens of *Trichophycus venosum* exhibiting occasional zones on fine paired scratch marks. 16f; side view of a U-shaped *Trichophycus venosum.*

scale bar = 1 cm

Plate 17

Miscellaneous arthropod trace fossils.

17a; *Diplichnites* form B grading into a *Diplichnites* form E at a sharp change in direction (arrowed). 17b; *Cruziana* ichnosp. 1 exhibiting more transverse and deeply impressed scratch marks on the inside of a sharp turn (arrowed). 17c; a short-section of strongly asymmetrical *Diplichnites* form D. 17d; ?*Protichnites*. 17e; *Diplichnites* form A grading into *Diplichnites* form D at a subtle change in trackway direction. 17f; *Diplichnites* form D (arrowed).

scale bar = 1 cm

Plate 18

Diplichnites.

18a; a short stretch of *Diplichnites* form A. 18b; *Diplichnites* form B that is transitional with *Rusophycus bilobatum*. This trace fossils was found as both an impression and matching cast. 18c; a short stretch of *Diplichnites* form A. 18d; an impression of a *Diplichnites* form B like trail made up of a number of *Rusophycus bilobatum*. 18e; a short *Diplichnites* grading into a *Rusophycus*. This trace fossil appears to represent a trilobite alighting on the sediment while in motion and subsequently digging into the sediment. 18f; *Diplichnites* form A (arrowed).

scale bar = 1 cm

Plate 19

Monomorphichnus.

19a; *Diplichnites* form D, strongly asymmetrical, double sets of scratch marks (arrowed). 19b; a long track way of *Monomorphichnus* form A (large arrow) with single scratch marks, and some single sets of *Monomorphichnus* form C (small arrow). 19c; *Monomorphichnus* for A grading into *Diplichnites* form A, grading back into *Monomorphichnus*. 19d; *Monomorphichnus* form B. 19e; a track way of *Monomorphichnus* form A with double scratch marks. 19f; a single set of *Monomorphichnus* form C.

scale bar: 10 cm a,b,c,e; 1 cm d,f

Plate 20

Didymaulichnus and *Monomorphichnus*.

20a; 10 mm wide *Didymaulichnus lyelli* from Moraine Lake. 20b; close up of *Didymaulichnus lyelli* with a change in cross-sectional morphology of a trail as it crosses another trail (from lower right corner in 20a). 20c; 5 mm wide *Didymaulichnus lyelli* from unit 4, showing a much higher depth to width ratio than the 10 mm wide form. 20d; 5 mm wide *Didymaulichnus lyelli* from unit 4. 20e; *Monomorphichnus* form B from Moraine Lake. 20f; *Monomorphichnus* form D from Moraine Lake.

scale bar = 2 cm

Plate 21

Rugosa-group *Cruziana.*

21a; lower bedding surface of a thin quartzite with abundant *Cruziana* ichnosp. 1, *Rusophycus* ichnosp. 3, and *Teichichnus*. Most of the *Rusophycus* are joined into strings of *Rusophycus* or with *Cruziana*. *Cruziana* are all less than 7 cm. 21b; a short, low relief *Cruziana* ichnosp. 1 showing the long bundled scratch marks. 21c; the scratch mark pattern of *Cruziana furcifera*: fine, paired, anastomosing scratch marks. 21d; expanded view of 21b, showing the density and overprinting of arthropod trace fossils. 21e; *Cruziana goldfussi* with very long, regular, near longitudinal scratch marks, grading into a slightly higher relief *Cruziana rugosa* with shorter scratch marks separated by transverse ridges (at the top of the picture. From float at Lake O'Hara. 21f; *Cruziana rugosa* with short sets of parallel, longitudinal scratch marks separated by transverse ridges.

scale bar = 2 cm

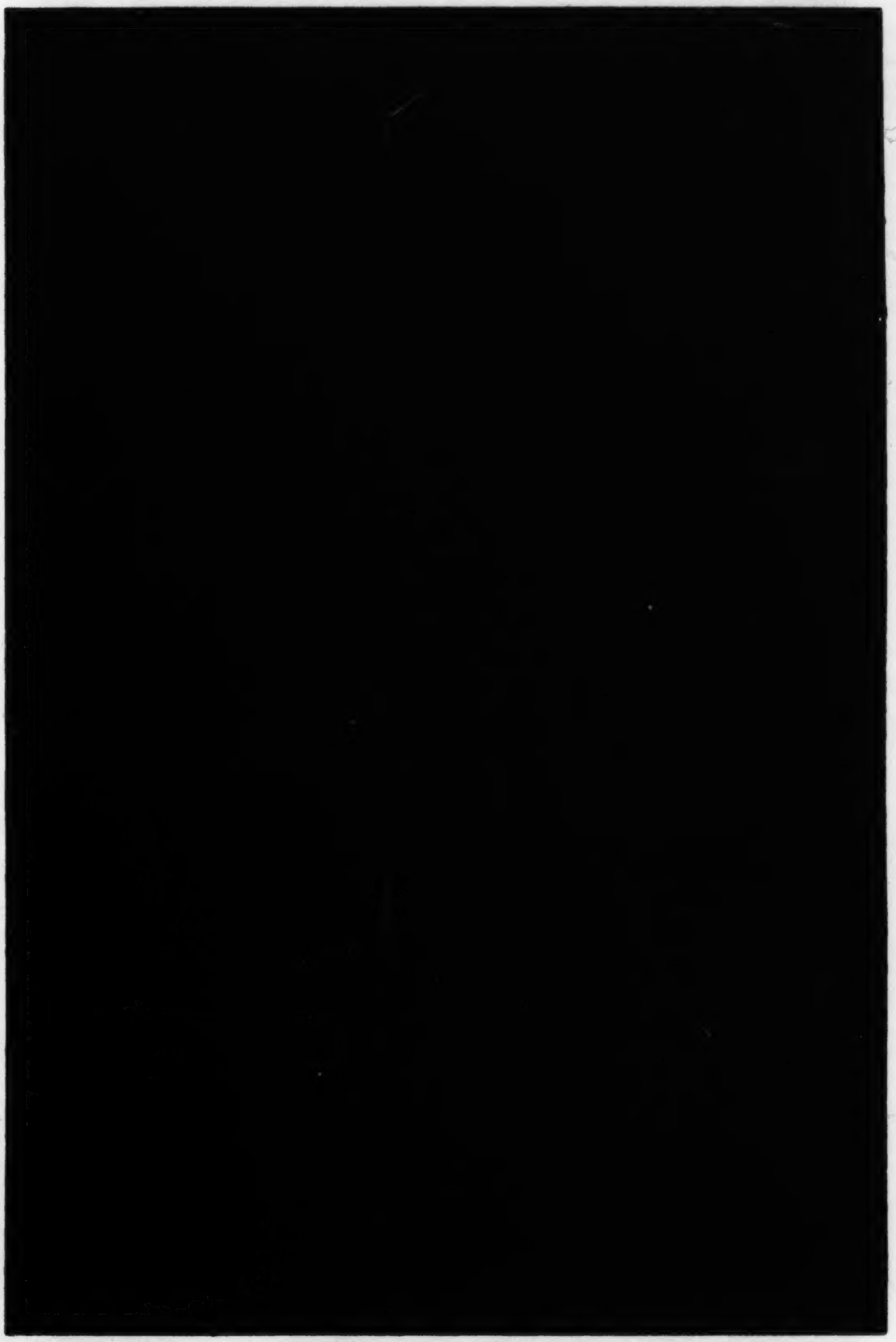


Plate 22

Small *Cruziana* with regular scratch marks.

22a, c; long trackways consisting of *Diplichnites* form B (large arrow), *Cruziana* ichnosp. 2 form A (single small arrow), and *Rusophycus bilobatum* (double small arrow). 22b; trackways of *Cruziana* ichnosp. 2 form B. 22d; *Cruziana problematica* showing the coarse, C-shaped scratch marks. 22e; *Cruziana* ichnosp. 3. 22f; *Cruziana stromnessa* showing scratch marks that are much finer than those in 22d.

scale bar = 1 cm

Plate 23

Deep furrowed *Cruziana*.

23a; transverse section through *Cruziana pormensis* (see 23c) showing the nearly circular cross-section indicative of true burrowing. 23b; *Cruziana clavata* showing a gently tapering termination. 23c; *Cruziana pormensis* showing the well developed lobes with fine, curving scratch marks and the horizontal ridges along the side. 23d; a long furrow or tunnel of *Cruziana clavata*. This long, strait habit is common in this ichnospecies. 23e; a blunt termination in a *Cruziana clavata*. The arrow points to tangential ridges though to indicate incremental turning on the part of the trace maker. 23f; *Cruziana plicata* showing the low relief lobes and straight to gently curving fine scratch marks spanning the width of the lobes.

scale bar = 1 cm

Plate 24

Semiplicata-group *Cruziana*.

24a; *Cruziana semiplicata* form A (top of picture) grading into a *Rusophycus bilobatum* and on into a *Cruziana* ichnosp. 4. The *Cruziana semiplicata* has fine, longitudinal striations on the lateral lobes rather than the coarser, more oblique scratch marks on the specimen in 24b. 24b; one half of a *Cruziana semiplicata* form A with strong oblique scratch marks on the lateral lobes. Some of these marks appear to be continuous with medial lobe scratch marks, however, this may just be coincidental overprinting. 24c; *Cruziana semiplicata* form B with the typical flat medial scratch marks (similar to Seilacher, 1970, plate 1c). 24d; *Cruziana arizonensis* with very high relief, well rounded lateral lobes and flat, low relief medial lobes, the outer edge of which are cross-cut by the lateral lobes. 24e; *Cruziana* ichnosp. 4 with close spaced, near transverse scratch marks, well rounded in cross-section, similar to *Rusophycus bilobatum*. 24f; a large basal bedding surface covered with *Cruziana* ichnosp. 4.

scale bar = 2 cm

Plate 25

Rusophycus.

25a, b; ***Rusophycus parallelum***, characterised by long, straight sided, blunt ended lobes. 25c; ***Rusophycus navicella***, an elongate weakly bilobed pit with irregular scratch marks. 25d; ***Rusophycus bilobatum*** form A, high relief well rounded lobes. 25e; ***Rusophycus bilobatum*** form B, low relief, flat lobes with a rectangular plan view shape. 25f; ***Rusophycus cerecedensis*** with well spaced, deeply impressed paired scratch marks.

scale bar = 1 cm

Plate 26

Fasciculata-type *Rusophycus*.

26a; *Rusophycus avalonensis* form B, a similar overall shape to *Rusophycus bilobata* but with fine scratch marks organised into fan-shaped groups. This sample is heavily overburrowed by *Planoites*, a common phenomenon in unit 2. 26b; side view of *Rusophycus jenningsi* showing the horizontal ridges on the steep sides, presumed to be caused by the shovelling action of the cephalon. 26c; top view of *Rusophycus jenningsi* showing the medial bunching of coarse scratch marks. 26d; top view of *Rusophycus jenningsi* showing a distinct front-to-back break in the scratch mark orientation (arrowed). 26e; a lower relief example of *Rusophycus avalonensis* form B than 26a, overburrowed by *Planolites montanus*. 26f; *Rusophycus avalonensis* form A, very low relief but with medial bunching of scratch marks clearly evident.

scale bar = 1 cm

Plate 27

Rusophycus.

27a; close up of *Rusophycus eutendorfensis* form B with a plan view shape similar to *Rusophycus parallelum.* 27b; *Rusophycus eutendorfensis* form B in a typical serial arrangement of pits. 27c; *Rusophycus eutendorfensis* form A with extremely fine, transverse scratch marks. 27d; a *Rusophycus* from the block in 21a. It has the overall form of *Rusophycus* ichnosp. 3, however, the scratch marks are much more deeply impressed. 27e; *Rusophycus* ichnosp. 3 from the block in 21a. The serial arrangement of *Rusophycus* of identical size indicates that one trace maker made all three in a row, most likely the result of a deposit feeding behaviour. 27f; *Rusophycus carinata* showing the lateral lobes with fine, longitudinal striations and the medial lobes with coarse, oblique scratch marks.

scale bar = 1 cm

Plate 28

Rusophycus.

28a; *Rusophycus* ichnosp. 2: long, straight sided structures that slope down to bedding at either end. 28b; one half of a *Rusophycus cerecedensis* showing the well spaced, deeply impressed, paired scratch marks. 28c; *Rusophycus* ichnosp. 1. 28d; *Rusophycus ?dispar*, a paired bundle of scratch marks without any distinct lobe structure. 28e, f (close up); *Rusophycus rugosa* with sets of short, mutually parallel, near longitudinal scratch marks separated by transverse ridges.

scale bar = 1 cm

REFERENCES

Aitken, J.D., (1969), Documentation of the sub - Cambrian unconformity, Rocky Mountains Main Ranges, Alberta, *Canadian Journal of Earth Sciences*, 6(2):193-200

Aitken, J.D., (1984), Strata and trace fossils near the Precambrian - Cambrian boundary, Mackenzie, Selwyn and Wernecke Mountains, Yukon and North West Territories: discussion, Geologic Survey of Canada, Paper 84-1B:401-407

Alpert, S.P., (1973), *Bergaueria prantl* (Cambrian and Ordovician), a probable actinian trace fossil, *Journal of Paleontology*, 47(5):919-924

Alpert, S.P., (1974), Systematic review of the genus *Skolithos*, *Journal of Paleontology*, 48(4):661-669

Alpert, S.P., (1976), Trilobite and star-like trace fossils from the White - Inyo mountains, California, Journal of Paleontology, 50(2):226-239

Alpert, S.P., (1977), Trace fossils and the basal Cambrian boundary, *in* Crimes, T.P. and Harper, J.C., eds., *Trace Fossils II*, *Geological Journal* special issue, 9:1-8, Seel House Press

Alpert, S.P. and Moore, J.M., (1975), Lower Cambrian trace fossil evidence for predation on trilobites, *Lethaia*, 8:223-230

Archer, A.W. and Maples, C.G., (1984), Trace fossil distribution across a marine-to-nonmarine gradient in the Pennsylvanian of southwestern Indiana, *Journal of Paleontology*, 58(2):448-467

Arnott, R.W., (1984), Proximal Channel Deposits of the Hadrynian Hector Formation, Lake Louise, Alberta, M.Sc. Thesis, University of Alberta, Edmonton, Alberta, Canada

Arnott, R.W. and Hein, F.J., (1986), Submarine canyon fills of the Hector Formation, Lake Louise Alberta: Late Precambrian syn-rift deposits of the proto Pacific miogeocline, Bulletin of Canadian Petroleum Geology, 34(4):395-407

Baldwin, C.T., (1976), Trace fossil stratigraphy of some shallow marine Cambro-Ordovician rocks from Brittany, N.W. Spain and the U.K., Ph.D. Thesis, Liverpool University, Liverpool, England

Baldwin, C.T., (1977)a, The stratigraphy and facies associations of trace fossils in some Cambrian and Ordovician rocks of north western Spain, *in* Crimes, T.P. and Harper, J.C., eds., *Trace Fossils II*, *Geological Journal* special issue, 9:9-40, Seel House Press

Baldwin, C.T., (1977)b, Internal structure of trilobite trace fossils indicative of an open surface furrow origin, *Palaeogeography Palaeoclimatology Palaeoecology*, 21:273-284

Banks, L., (1970), Trace fossils from the late Precambrian and Lower Cambrian of Finnmark, Norway, *in* Crimes, T.P. and Harper, J.C., eds., *Trace Fossils*, *Geological Journal* special issue, 3:19-34, Seel House Press

Barnes, R.D., (1980), *Invertebrate Zoology*, Saunders College, 1089 p.

Bergström, J., (1970), *Rusophycus* as an indication of early Cambrian age, *in* Crimes, T.P. and Harper, J.C., eds., *Trace Fossils, Geological Journal* special issue, 3:35-42, Seel House Press

Bergström, J., (1972), Appendage morphology of the trilobite *Cryptolithus* and its implications, *Lethaia*, 5:85-94

Bergström, J., (1973), Organization, life, and systematics of trilobites, *Fossils and Strata*, 2, 69 pp.

Bergström, J., (1976), Lower Paleozoic trace fossils from eastern Newfoundland, *Canadian Journal of Earth Sciences*, 13:1613-1633

Bergström, J., (1980), Morphology and systematics of early arthropods, *Abhandlungen. Naturwissenschaftlichen Verins zu Hamburg*, 23:7-42

Bergström, J. and Brassel, G., (1984), Legs of the trilobite *Rhenops* from the Lower Devonian Hunsrück Slate, *Lethaia*, 4:303-319

Birkenmajer, K. and Brunton, D.L., (1971), Some trilobite resting and crawling traces, *Lethaia*, 4:303-319

Boardman, R.S., Cheetham, A.H., and Rowell, A.J., (1987), *Fossil Invertebrates*, Blackwell Scientific Publications, 713 pp.

Boggs, S.jr., (1987), *Principles of Sedimentology and Stratigraphy*, Merrill, 784 pp.

Bradshaw, M.A., (1981), Paleoenvironmental interpretations and systematics of Devonian trace fossils from the Taylor Group (lower Beacon Supergroup), Antarctica, *New Zealand Journal of Geology and Geophysics*, 24:615-652

Bromley R.G. and Asgaard, U., (1979), Triassic freshwater ichnocoenoces from Carlsberg Fjord, East Greenland: *Palaeogeography Palaeoclimatology Palaeoecology*, 28:39-80

Bromley R.G. and Ekdale, A.A., (1984), *Chondrites*: a trace fossil indicator of anoxia in sediments, *Science*, 224:872-874

Bromley, R.G. and Frey, R.W., (1974), Redescription of the trace fossil *Gyrolithes* and taxonomic evaluation of *Thalassinoides*, *Ophiomorpha* and *Spongeliomorpha*, *Bulletin of the Geological Society of Denmark*, 23:311-335

Chamberlain, C.K., (1971), Morphology and ethology of trace fossils from the Ouachita Mountains, southeast Oklahoma, *Journal of Paleontology*, 15(2):212-246

Chamberlain, C.K., (1975), Trace fossils in DSDP cores of the Pacific, *Journal of Paleontology*, 49:1074-1096

Chamberlain, C.K., (1977), Ordovician and Devonian trace fossils from Nevada, Nevada Bureau of Mines and Geology, Bulletin 90:1-24

Charlesworth, H.A.K., Weiner, J.L., Akehurst, A.J., Bielenstein, H.U., Evans, C.R., Griffiths, R.E., Remington, D.B., Stauffer, M.R., and Steiner, J., (1967), Precambrian geology of the Jasper region, Alberta, Research Council of Alberta

Bulletin, 23, 74 pp.

Cisne, J.L., (1981), *Triarthrus eatoni* (Trilobita): anatomy of its exoskeletal, skeletomuscular, and digestive systems, *Palaeontographica Americana*, 9(53):99-142

Clark, R.B., (1979), Radiation of the metazoa, *in* House, M.B., ed., *The Origin of Major Invertebrate Groups*, Academic Press, pp. 55-101

Clarkson, E.N.K., (1979), *Invertebrate Paleontology and Evolution*, George Allan & Unwin, chapter 11, pp. 258-292

Clausen, C.K. and Vilhjalmsson, M., (1986), Substrate control of Lower Cambrian trace fossils from Bornholm Denmark, *Palaeogeography PalaeoclimatologyPalaeoecology*, 56:51-68

Collinson, J.D. and Thompson, D.B., (1982), *Sedimentary Structures*, George Allen and Unwin

Conway Morris, S., (1987), The search for the Precambrian-Cambrian boundary, *American Scientist*, 75:157-167

Covich, A.P., (1976), Analysing shapes of foraging areas: some ecological and economic theories, *Annual Review of Ecological Systematics*, 7:235-257

Cowie, J.W. and Spencer, A.M., (1970), Trace fossils of the late Precambrian and Lower Cambrian of east Greenland, *in* Crimes, T.P. and Harper, J.C., eds., *Trace Fossils, Geological Journal* special issue, 3:91-100, Seel House Press

Crimes, T.P., (1968), *Cruziana*: a stratigraphically useful trace fossil, *Geological Magazine*, 105(4):360-364

Crimes, T.P., (1969), Trace fossils from the Cambro-Ordovician of North Wales and their stratigraphic significance, *Geological Journal*, 6(2):333-338

Crimes, T.P., (1970)a, A facies analysis of the Cambrian of Wales, *Palaeogeography Palaeoclimatology Palaeoecology*, 7:113-170

Crimes, T.P., (1970)b, The significance of trace fossils in sedimentology, stratigraphy, and palaeoecology with examples from lower Paleozoic strata, *in* Crimes, T.P. and Harper, J.C., eds., *Trace Fossils*, *Geological Journal* special issue, 3:101-126, Seel House Press

Crimes, T.P., (1970)c, Trilobite tracks and other trace fossils from the Upper Cambrian of North Wales, *Geological Journal*, 7:47-68

Crimes, T.P., (1974), Colonization of the early ocean floor, *Science*, 248:328-330

Crimes, T.P., (1975)a, Trilobite traces from the lower Tremadoc of Tortworth, *Geological Magazine*, 112(1):33-46

Crimes, T.P., (1975)b, The production and preservation of trilobite resting and furrowing traces, *Lethaia*, 8:35-48

Crimes, T.P., (1975)c, The stratigraphic significance of trace fossils, *in* Frey, R.W., ed., *The Study of Trace Fossils*, Springer-Verlag, pp. 109-130

Crimes, T.P., (1987), Trace fossils and the correlation of the late Precambrian and Early Cambrian strata, *Geological Magazine*, 124(2):97-119

Crimes, T.P. and Anderson, M.M., (1985), Trace fossils from the late Precambrian-Early Cambrian strata of southeastern Newfoundland (Canada): temporal and environmental implications, *Journal of Paleontology*, 59(2):310-343

Crimes, T.P. and Germs, G.J.B., (1982), Trace fossils of the Nama Group (Precambrian-Cambrian) of southwest Africa (Namibia), *Journal of Paleontology*, 56:890-907

Crimes, T.P., Goldring, R., Homewood, P., Stuijvenberg, J. van, and Winkler, W., (1981), Trace fossil assemblages of deep-sea fan deposits, Gurnigel and Schlieren flysch (Cretaceous-Eocene), Switzerland, *Eclogae Geologicae Helvetiae*, 74:953-995

Crimes, T.P., Legg, I., Marcos, A., and Arboleya, M., (1977), ?Late Precambrian-low Lower Cambrian trace fossils from Spain, *in* Crimes, T.P. and Harper, J.C., eds., *Trace Fossils II*, *Geological Journal* special issue, 9:91-138, Seel House Press

Crimes, T.P. and Marcos, A., (1976), Trilobite traces and the age of the lowest part of the Ordovocian reference section for N.W. Spain, *Geological Magazine*, 113(4):349-356

Culver, S.J., Buzas, M.A., and Collins, L.S., (1987), On the value of taxonomic standardization in evolutionary studies, *Paleobiology*, 13(2):169-176

Demathieu, G.R., (1985), Trace fossil assemblages in middle Triassic marginal marine deposits, eastern boarder of the Massif Central, France, *in* Curran, H.A., ed., *Biogenic Structures: their use in interpreting depositional environments*, SEPM special publication, 35:53-66

Deiss, C., (1940), Lower and Middle Cambrian stratigraphy of southwestern Alberta and southeastern British Columbia, Geological Survey of America Bulletin, 51:731-794

Eagar, R.M.C., Baines, J.G., Collison, J.D., Hardy, P.G., Okolo, S.A., and Pollard, J.E., (1985), Trace fossil assemblages and their occurrence in Silesian (mid-Carboniferous) deltaic sediments of the central Pennine Basin, England, *in* Curran, H.A., ed., *Biogenic Structures: their use in interpreting depositional environments*, SEPM special publication, 35:99-149

Ekdale, A.A., Bromley, R.G., and Pemberton, S.G., (1984), *Ichnology, trace fossils in sedimentology and stratigraphy*, SEPM short coarse 15

Eldredge, N., (1970), Observations on burrowing behavior in *Limulus polyphemus* (Chelicerata, Merostomata), with implications on the functional anatomy of trilobites, *American Museum Novitates*, 2436:1-17

Eldredge, N., (1971), Patterns of cephalic musculature in the Phacopina (Trilobita) and their significance, *Journal of Paleontology*, 45:52-67

Elliott, D.K. and Martin, D.L., (1987), A new trace fossil from the Cambrian Bright Angel Shale, Grand Canyon, Arizona, *Journal of Paleontology*, 61(4):641-648

Elliott, T., (1986), Siliciclastic Shorelines, *in* Reading, H.G., ed., *Sedimentary Environments and Facies*, Blackwell Scientific Publications, chapter 7, pp. 155-188

Esakova, N.V., (1988), Precambrian-Cambrian boundary problem on the Siberian Platform, in Landing, E. and Narbonne, G.M., eds., Trace fossils, small shelly fossils, and the Precambrian-Cambrian boundary, Proceedings, *New York State Meuseum Bulletin*, 436

Fedonkin, M.A., (1978), Ancient trace fossils and the evolution of mud-eaters, *Paleontology Journal*, 2:241-246

Fedonkin, M.A., (1980), Early stages of evolution of metazoa on the basis of paleoichnological data, *Izvestia Academii Nauka SSR*, series geologie 2:226-233

Fenton, C.R. and Fenton, M.A., (1937), Trilobite "nests" and feeding burrows, *American Midland Naturalist*, 18:446-451

Fillion D. and Pickerill, R.K., (1984), Systematic ichnology of the middle Ordovician Trenton Group, St. Lawrence Lowland, eastern Canada, *Maritime Sediments and Atlantic Geology*, 20(1):1-41

Fisher, W.A., (1978), Trace fossils of the lower Harding Formation (Middle Ordovician), Colorado, *in* Pruit, J.D. *et al.*, eds., *Energy Resources of the Denver Basin*, Rocky Mountain Association of Geologists, Field Conference Guidebook, pp. 191-197

Fortey, R.A., (1985), Pelagic trilobites as an example of deducing the life habits of extinct arthropods, *Transactions of the Royal Society of Edinburgh*, 76:219-230

Fox, R.W., (1986), Species in paleontology, *Paleoscene*, 1:73-84

Frey, R.W. and Howard, J.D., (1985), Trace fossils of the Panther Member, Star Point Formation (Upper Cretaceous), Coal Creek Canyon, Utah, *Journal of Paleontology*, 59:370-404

Frey, R.W. and Pemberton, S.G., (1984), Trace fossil facies models, *in* Walker, R.G., ed., *Facies Models*, Geoscience Canada reprint series 1, pp. 189-207

Fritz, W.H., (1980)a, Two new formations in the Lower Cambrian Atan Group, Cassiar Mountains, north - central British Columbia, *in* Current Research, Part B, Geologic Survey of Canada, Paper 80-1B:217-225

Fritz, W.H., (1980)b, International Precambrian-Cambrian Boundary Working Group's 1979 field study to Mackenzie Mountains, Northwest Territories, Canada, *in* Current Research, Part A, Geological Survey of Canada, Paper 80-1A:41-45

Fritz, W.H. and Crimes, T.P., (1985), Lithology, trace fossils and correlation of Precambrian-Cambrian boundary beds, Cassiar Mountains, north central British Columbia, Geological Survey of Canada, Paper 83-13

Fritz, W.H., Narbonne, G.M., and Gordey, S.P., (1983), Strata and trace fossils near the Precambrian - Cambrian boundary, Mackenzie, Selwyn, and Wernecke mountains, Yukon and Northwest territories, *in* Current Research, Part B, Geological Survey of Canada, Paper 83-1B:41-45

Fürsich, F.T., (1974)a, On *Diplocraterion* Torell 1870 and the significance of morphological features in vertical spreiten-bearing, U-shaped trace fossils, *Journal of Paleontology*, 48(5):952-962

Fürsich, F.T., (1974)b, Ichnogenus *Rhizocorallium*, *Paläontologische Zeitschrift*, 48:16-28

Goldring, R., (1962), The trace fossils of the Baggy Beds (Upper Devonian) of North Devon, England, *Paläontologische Zeitschrift*, 36:232-251

Goldring, R., (1985), The formation of the trace fossil *Cruziana*, *Geological Magazine*, 122(1):65-72

Goodwin, P.W. and Anderson, E.J., (1974), Associated physical and biogenic structures in environmental subdivision of a Cambrian tidal sand body, *Journal of Geology*, 82:779-794

Gould, J.L., (1982), *Ethology: The Mechanisms and Evolution of Behavior*, Norton, 544 pp.

Gureyev, Yu. A., (1985), The nature of the taxon in paleoichnology, *Paleontological Journal*, 19(4):118-120

Hakes, W.G., (1976), Trace fossils, and deposition environment of four clastic units, Upper Pennsylvanian megacyclothems, northeast Kansas, *University of Kansas Paleontological Contributions*, 36, 46 pp.

Hakes, W.G., (1985), Trace fossils from brackish-marine shales, upper Pennsylvanian of Kansas, U.S.A., *in* Curran, H.A., ed., *Biogenic Structures: their use in interpreting depositional environments*, SEPM special publication, 35:21-35

Hallam, A. and Swett, K., (1966), Trace fossils from the Lower Cambrian pipe rock of the north-west Highlands, *Scottish Journal of Geology*, 2(1):101-106

Häntzschel, W., (1975), Trace Fossils and Problematica, *in* Teichert, C., ed., *Treatise on Invertebrate Paleontology*, Part W, Miscellanea, Supplement 1, The Geological Society of America, 269 pp.

Harland, W.B., Cox, A.V., Llewellyn, P.G., Pickton, C.A.G., Smith, A.G., and Walters, R., (1982), *A Geologic Time Scale*, Cambridge University Press

Heezen, B.C. and Hollister, C.D., (1971), *Face of the Deep*, Oxford University Press, 659 pp.

Jordan, D.W., (1985), Trace fossils and depositional environments of Upper Devonian black shales, east-central Kentucky, U.S.A., *in* Curran, H.A., ed., *Biogenic Structures: their use in interpreting depositional environments*, SEPM special publication, 35:279-298

Kolb, S. and Wolf, R., (1979), Distribution of *Cruziana* in the lower Ordovician sequence of Celtiberia (NE Spain) with a revision of the *Cruziana rugosa*-group, *Neues Jahrbuch fur Geologie Paläontologie Monatschefte*, 8:457-474

Ksiazkiewicz, M., (1977), Trace fossils in the flysch of the Polish Carpathians, *Palaeontologica Polonica*, 36

Landing, E. and Brett, C.E., (1987), Trace fossils and regional significance of a middle Devonian (Givetian) disconformity in southwestern Ontario, *Journal of Paleontology*, 61(2):205-230

Legg, I.C., (1985), Trace fossils from a middle Cambrian deltaic sequence, north Spain, *in* Curran, H.A., ed., *Biogenic Structures: their use in interpreting depositional environments*, SEPM special publication, 35:151-165

Martinsson, A., (1970), Toponomy of trace fossils, *in* Crimes T.P. and Harper, J.C., eds., *Trace Fossils, Geological Journal* special issue, 3:323-330, Seel House Press

McMenamin, M.A.S., (1987), The emergence of animals, *Scientific American*, 256(4):94-102

Miller, M.F. and Knox, L.W., (1985), Biogenic structures and depositional environments of a Lower Pennsylvanian coal-bearing sequence, Northern Cumberland Plateau, Tennessee, U.S.A., *in* Curran, H.A., ed., *Biogenic Structures: their use in interpreting depositional environments*, SEPM special publication, 35:67-97

Müller, K.J. and Walossek, D., (1987), Morphology, ontogeny, and life habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden, *Fossils and Strata*, 19, 124 pp.

Narbonne, G.M., (1984), Trace fossils in Upper Silurian tidal flat to basin slope carbonates of arctic Canada, *Journal of Paleontology*, 58:398-415

Narbonne, G.M., Myrow, P.M., Landing E., and Anderson, M.M., (1987), A candidate stratotype for the Precambrian-Cambrian boundary, Fortune Head, Burin Peninsula, southeastern Newfoundland, *Canadian Journal of Earth Sciences*, 24(7):1277-1293

Nowlan, G.S., Narbonne, G.M., and Fritz, W.H., (1985), Small shelly fossils and trace fossils near the Precambrian-Cambrian boundary in the Yukon Territory, Canada, *Lethaia*, 18:233-256

Nybakken, J.W., (1982), *Marine Biology, an ecological approach*, Harper and Row, pp. 127-151

Orlowski, S., Radwanski, A., and Roniewicz, P., (1970), The trilobite ichnocoenoces in the Cambrian sequences of the Holy Cross Mountains, *in* Crimes, T.P. and Harper, J.C., eds., *Trace Fossils, Geological Journal* special issue, 3:345-360, Seel House Press

Osgood, R.G., (1970), Trace fossils of the Cincinnati area, *Palaeontographica Americana*, 6(41):281-444

Osgood, R.G. (1975), The paleontological significance of trace fossils, *in* Frey, R.W., ed., *The Study of Trace Fossils*, Springer Verlag, pp. 87-108

Osgood, R.G. and Drennen, W.T., (1975), Trilobite trace fossils from the Clinton Group (Silurian) of east-central New York State, *Bulletin of American Paleontology*, 287:299-348

Palonen, P.A., (1976), Sedimentology and stratigraphy of Gog Group sandstones in southern Canadian Rockies, Ph.D. Thesis, University of Calgary, Calgary, Alberta, Canada

Pemberton, S.G. and Frey, R.W., (1982), Trace fossil nomenclature and the *Planolites-Palaeophycus* dilemma, *Journal of Paleontology*, 56(4):843-881

Pemberton, S.G., Frey, R.W., and Bromley, R.G., (1988), The taxonomy of *Conostichus* and other plug-shaped ichnofossils, *Canadian Journal of Earth Sciences*, 25:866-892

Pickerill, R.K., (1977), Trace fossils from the Upper Ordovician (Caradoc) of the Berwyn Hills, Central Wales, *Geological Journal*, 12(1):1-16

Pickerill, R.K., (1981), Trace fossils in a Lower Palaeozoic submarine canyon sequence - the Siegas Formation of northwestern New Brunswick, Canada, *Maritime Sediments and Atlantic Geology*, 17:37-58

Pickerill, R.K., Romano, M., and Melendez, B., (1984), Arenig trace fossils from the Salamanca area, western Spain, *Geological Journal*, 9:249-269

Pienkowski, G., (1985), Early Liassic trace fossil assemblages from the Holy Cross Mountains, Poland: their distribution in continental and marginal marine environments, *in* Curran, H.A., ed., *Biogenic Structures: their use in interpreting depositional environments*, SEPM special publication, 35:37-52

Plicka, M., (1970), *Zoophycos* and similar fossils, *in* Crimes T.P. and Harper, J.C., eds., *Trace Fossils*, *Geological Journal* special issue, 3:361-370, Seel House Press

Pollard, J.E., (1981), A comparison between Triassic trace fossils of Cheshire and south Germany, *Palāeontology*, 24:555-588

Pollard, J.E., Steel, R.J., and Undersrud, E., (1982), Facies sequences and trace fossils in lacustrine/fan delta deposits, Hornelen Basin (M. Devonian), western Norway, *Sedimentary Geology*, 32:63-87

Price, R.A., Cook, D.G., Aitken, J.D., and Mountjoy, E.W., (1980)a, Lake Louise (East Half), 1:50,000 Geological Map, Geological Survey of Canada, Map 1482A

Price, R.A., Cook, D.G., Aitken, J.D., and Mountjoy, E.W., (1980)b, Lake Louise (West Half), 1:50,000 Geological Map, Geological Survey of Canada, Map 1483A

Radwanski, A. and Roniewicz, P., (1963), Upper Cambrian trilobite ichnocoenoses from Wielka Wisniowka (Holy Cross Mountains, Poland), *Acta Palaeontologica Polonica*, 8:259-280

Rasetti, F., (1951), Middle Cambrian stratigraphy and faunas of the Canadian Rocy Mountains, Smithsonian Miscellaneous Collections, 116(5), 277 pp.

Ratcliffe, B.C. and Fagerstrom, J.A., (1980), Invertebrate lebensspuren of Holocene flood plains: their morphology, origin, and paleoecological significance, *Journal of Paleontology*, 54:614-630

Reineck, H.E. and Singh, I.B., (1975), *Depositional Sedimentary Environments*, Springer-Verlag

Runnegar, B., (1982), Oxygen requirements, biology and phylogenetic significance of the late Precambrian worm *Dickinsonia*, and the evolution of the burrowing habit, *Alcheringa*, 6:223-239

Scotese, C.R., Bamback, R.K., Barton, C. van der Voo, R., and Ziegler, A.M., (1970), Paleozoic base maps, *Journal of Geology*, 87:217-277

Seilacher, A., (1955), Spuren und fazies in Unterkamrium, *in* Schindewolf, O.H. and Seilacher, A., eds., *Beitrage zur Kenntnis des Kambriums, in der Salt Range* (*Pakistan*). Akademie der Wissenschaften und der Literature zu Mainz, mathermatisch- naturwissenschaftliche Klasse, Abhandlungen, 10:11-143

Seilacher, A., (1962), Form und funktion des trilobiten-daktylus, *Paläontologische Zeitschrift*, 36:218-227

Seilacher, A., (1964), Biogenic sedimentary structures, *in* Imbrie, J. and Newell, N., eds., *Approaches to Paleoecology*, John Wiley, pp. 296-316

Seilacher, A., (1967), Bathymetry of trace fossils, *Marine Geology*, 5:413-428

Seilacher, A., (1970), *Cruziana* stratigraphy of "non fossiliferous" Paleozoic sandstones; *in* Crimes, T.P. and Harper, J.C., eds., *Trace Fossils, Geological Journal* special issue, 3:447-476

Seilacher, A., (1974), Flysch trace fossils: evolution of behavioral diversity in the deep-sea, *Neues Jahrbuch fur Geologie Paläontologie Monatschefte*, 4:233-245

Seilacher, A., (1977)a, Evolution of trace fossil communities, *in* Hallam, A., ed., *Patterns of Evolution*, Elsevier, pp. 359-376

Seilacher, A., (1977)b, Pattern analysis of Paleodictyon and related trace fossils, *in* Crimes, T.P. and Harper, J.C., eds., *Trace Fossils II, Geological Journal* special issue, 9:289-334, Seel House Press

Seilacher, A., (1983), Upper Paleozoic trace fossils from the Gilf Kebir - Abu Ras area in southeastern Egypt, *Journal of African Earth Sciences*, 1:21-34

Seilacher, A., (1985), Trilobite palaeoecology and substrate relationships, *Transactions Royal Society of Edinburgh*, 76:231-237

Seilacher, A. and Crimes, T.P., (1969), "European" species of trilobite burrows in eastern Newfoundland, *in* Marshall Kay, ed., *North Atlantic Geology and Continental Drift*, American Association of Petroleum Geologists, Memoir 12:145-148

Shone, R.W., (1979), "Giant *Cruziana* from the Beaufort Group", *Transactions of the Geological Society of South Africa*, 82:371-375

Simpson, S., (1970), Notes on *Zoophycos* and *Spirophyton*, *in* Crimes, T.P. and Harper J.C., eds., *Trace Fossils, Geological Journal* special issue, 3:505-514, Seel House Press

Smith, A.B. and Crimes, T.P., (1983), Trace fossils formed by heart urchins - a study of *Scolicia* and related traces, *Lethaia*, 16:79-92

Speyer, S.E., (1988), Biostratinomy and functional morphology of enrollment in two Middle Devonian trilobites, *Lethaia*, 21:121-138

Stürmer, W. and Bergström, J., (1973), New discoveries on trilobites by X-rays, *Paläontologische Zeitschrift*, 47:101-141

Thayer, C.W., (1983), Sediment-mediated biological disturbance and the evolution of marine benthos, *in* Tevesz, M.J.S. and McCall, P.L., eds., *Biotic Interactions in Recent and Fossil Benthic Communities*, Plenum Press, pp. 480-626

Trewin, N.J., (1976) *Isopodichnus* in a trace fossil assemblage from the Old Red Sandstone, *Lethaia*, 9:29-37

Vossler, S.M., Magwood, J.P.A., and Pemberton, S.G., The youngest occurrence of the ichnogenus *Didymaulichnus* from the Upper Cretaceous (Turonian) Cardium Formation, *Journal of Paleontology*, in press

Vossler, S.M. and Pemberton, S.G., (1988), Superabundant *Chondrites*: a response to storm buried organic material?, *Lethaia*, 21(1), in press

Vossler, S.M. and Pemberton, S.G., *Skolithos* in the Upper Cretaceous Cardium Formation: an ichnological example of opportunistic ecology, *Lethaia*, in press

Walcott, C.D., (1890), The fauna of the lower Cambrian or *Olenellus* zone, *US Geological Survey Annual Report*, 10(1):509-774

Webby, B.D., (1970), Late Precambrian trace fossils from New South Wales, *Lethaia*, 3:79-109

Webby, B.D., (1973), Trace fossils from the Lintiss Vale Formation of New South Wales: a late Precambrian fauna, *Search*, 4:494-496

Webby, B.D., (1984), Precambrian-Cambrian trace fossils from western New South Wales, *Australian Journal of Earth Sciences*, 31:427-437

Whittington, H.B., (1980), Exoskeleton, moult stage, appendage morphology, and habits of the Middle Cambrian trilobite *Olenoides serratus*, *Palaeontology*, 23(1):171-204

Whittington, H.B. and Almond, J.E., (1987), Appendages and habits of the Upper Ordovician trilobite *Triarthrus eatoni*, *Philosophical Transactions of the Royal Society of London* B, 317:1-46

Wolberg, A.C., (1986), Sedimentology of the Lower Cambrian Gog Group, British Columbia: an Early Cambrian tidal deposit, M.Sc. Thesis, University of Alberta, Edmonton, Alberta, Canada

Young, F.G., (1972), Early Cambrian and older trace fossils from the southern cordillera of Canada, *Canadian Journal of Earth Sciences*, 9(1):1-17

Young, F.G., (1979), The lowermost Paleozoic McNaughton Formation and equivalent Cariboo Group of eastern British Columbia: Piedmont and tidal complex, Geological Survey of Canada, Bulletin 288:1-60

Zell, P.D., (1988), Burrowed *Phacops rana* from the Moscow Formation of New York, *Journal of Paleontology*, 62(2):311-312

Zhang Qin-Wen, Xu Dao-Yi, Sun Ying, Yang Zhengzhong, and Chai Zhifang, (1987), The rare event at the Precambrian-Cambrian boundary and the stratigraphic position of this boundary, *Modern Geology*, 11:69-77